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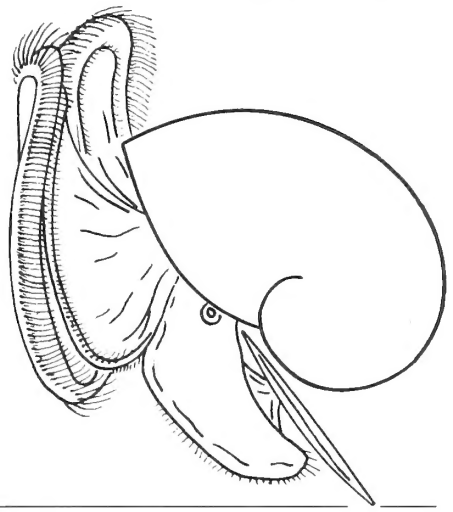
THE VELIGER



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Very short papers, generally not over 750 words, will be published in a "Notes, Information & News" column; in this column will also appear notices of meetings and other items of interest to our members and subscribers.

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The Veliger 41(1):1–132 (January 2, 1998)

A Systematic Review of the Hydrobiid Snails (Gastropoda: Rissooidea) of the Great Basin, Western United States. Part I. Genus *Pyrgulopsis*

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Abstract. A recently completed field survey of springs throughout the Great Basin yielded collections of hydrobiid snails from more than 500 sites, and revealed a wealth of undescribed diversity of these small gastropods. In this, the first of a two-part taxonomic series treating this material, 58 new species of *Pyrgulopsis* Call & Pilsbry, 1886, are described; and new records are provided for 10 previously described members of this genus. Assignment of these novelties to *Pyrgulopsis* is done with the acknowledgement that this large genus, as currently constituted, is probably not monophyletic, but a more refined classification of these snails reflecting evolutionary relationships must await preparation of a phylogenetic analysis, which is beyond the scope of this work. *Pyrgulopsis* occur in a variety of spring-fed water bodies in the Great Basin, including brackish and/or thermal habitats. Although a few species are widespread in the region, local endemism is prevalent and 22 of the new species are known only from single localities. Several areas contain concentrations of locally endemic snails which may represent species flocks, notably Duckwater Valley (seven species) and southern Steptoe Valley (five species). This fauna is largely distributed in an allopatric fashion, although a few springs harbor two or three species. Most of the springs inhabited by hydrobiids in the region are small, fishless, and have been ignored by state and federal land management agencies. However, many of these sites are degraded by livestock grazing, water withdrawal, and other activities and will require protection in order to conserve snails and other native aquatic biota. Two of the novelties described herein have become extinct during the past two decades.

> . . . the western states appear to present a set of conditions that should encourage isolation and speciation, especially in certain taxa containing macroscopic forms and the West should theoretically have a unique population of freshwater invertebrates. . . . Indeed, there is already evidence to show that the western aquatic invertebrate fauna is much richer and more varied than is indicated in the literature. (Pennak, 1958:224)

INTRODUCTION

Pennak's assertion that the aquatic invertebrate fauna of the western United States is undersampled was accompanied by a plea for colleagues to pursue more field, laboratory, and zoogeographic work in the region and publish the results of these endeavors. Although his prediction has been affirmed by the unabated publication of new taxa from the region over the past 28 years (e.g., Holsinger, 1974; Holsinger & Longley, 1980; Taylor, 1987), large areas in the West still have not been comprehensively surveyed and various aquatic invertebrate groups remain poorly known. Among the latter are the ubiquitous, locally abundant (Noel, 1954), small freshwater gastropods of the family Hydrobiidae, which total about 100 described species in the West. These snails are tightly linked with their aquatic habitat and often are endemic to single water bodies (particularly springs) or local drainage systems, features which render the group eminently suitable for zoogeographic inquiry (Taylor & Bright, 1987) and also thrust them into prominence with respect to ongoing efforts to conserve and manage western aquatic ecosystems. Much of this snail fauna now is imperiled—although a few species have been added to the Federal List of Threatened and Endangered Wildlife, a more telling indication of the status of the fauna is the fact that until recently, when the U.S. Fish and Wildlife Service discontinued designation of Category 2 species as candidates (USDI, 1996), most of these snails were candidates for addition to this list (e.g., USDI, 1994).

Although western hydrobiids are poorly known, the fauna of the Great Basin, in particular, has been neglected. This huge (500,000 km^2), remote and relatively rugged region is composed of more than 100, typically isolated, drainage basins (Mifflin, 1988:fig. 3) that were variously integrated during the wetter or pluvial period of the Late Quaternary (11,000–13,000 ybp) when many large lakes or wetlands were present (Figure 1). Although about 40 nominal species of hydrobiids have been recorded from the region, the group has not figured prominently in the few faunal surveys of the region (e.g., Brues, 1928, 1932), and published collections are from relatively few, widely scattered locales. Field coverage has been extremely uneven as, for instance, the Great

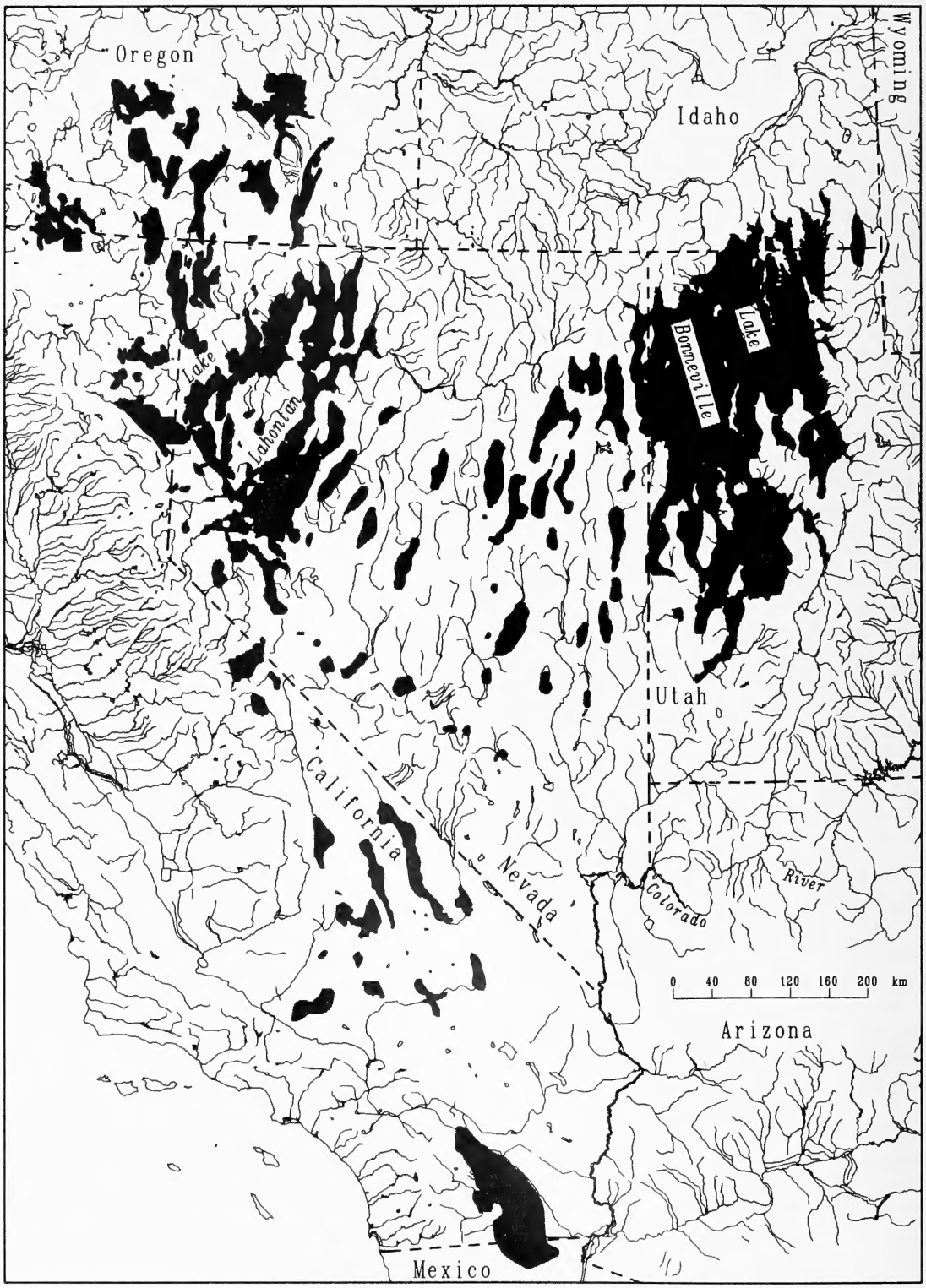


Figure 1

Map showing pluvial lakes (black) of the Great Basin superimposed on modern drainage (lake distribution from Mifflin & Wheat, 1979; King, 1982; Currey et al., 1983; Williams & Bedinger, 1984).

Basin of Utah was relatively well surveyed by Chamberlin, Jones, and other workers, while Nevada scarcely has been touched. However, the literature also provides indications that much fauna remains to be described (e.g., Deacon et al., 1980; J. E. Williams et al., 1985; Taylor & Bright, 1987:241). The paucity of collecting activity has important biogeographic implications as, for instance, the widely cited "fish hook" pattern, a distributional track attributed to various mollusks (and fishes) and extending from the eastern Bonneville Basin via the middle Snake River and western Lahontan basin to the Death Valley system (Taylor, 1960:figs. 1–3; Taylor, 1966a:fig. 7; Smith, 1981) may reflect inadequate sampling in the Great Basin of northern Nevada. Furthermore, most of the previous work on this fauna was published prior to the advent of modern approaches to gastropod systematics, and consisted of descriptions of single species based on empty shells. Many shell characters have proven unreliable, and hence these treatments are of limited utility today. The minimal attention paid to the hydrobiid snails of the Great Basin may be partly attributable to an impression that the desert basins of this region are largely devoid of aquatic biota: note that a large, fishless portion of south-central Nevada was named the "area of sterile basins" by Hubbs & Miller (1948:45).

There is an urgent need for discovery and documentation of these snails, as the typical habitats of Great Basin hydrobiids, very small springs that are often less than 1 m wide and 1 cm deep, are fragile, unprotected, and prone to extreme degradation owing to water development in the region, particularly livestock grazing. To fulfill this need and generate a biogeographic database I began field survey in 1985 of the Death Valley system, a large pluvial drainage in southwestern Nevada and southeastern California. Completion of this survey led to the description of 19 new species of hydrobiids from the region (Hershler & Sada, 1987; Hershler, 1989; Hershler & Pratt, 1990). Field survey then shifted to the remaining portions of the Great Basin in California, which led to discovery of an additional three new species (Hershler, 1995). From 1991–1995, a survey of the rest of the hydrographic Great Basin[1] was conducted. This included portions of Idaho, Nevada (exclusive of previously visited portions of the Death Valley system), Oregon, Utah, and Wyoming. Drainages of the Colorado River and Snake River in Nevada also were visited. During the survey more than 2000 sites were visited. Hydrobiid snails were collected from more than 500 springs, and many new taxa were discovered. The purpose of this paper, the first of a two-part taxonomic series, is to describe the new material of *Pyrgulopsis* Call & Pilsbry, 1886, the largest genus of hydrobiids in North America. In a recent review (Hershler, 1994), I recognized 65 Recent species in *Pyrgulopsis*; eight more new species have since been introduced (Hershler, 1995; Thompson, 1995). Herein an additional 58 new species are described, as are numerous new records for 10 previously described members of this genus.

Novelties described herein are allocated to *Pyrgulopsis* in the broad sense utilized by Hershler (1994). Note that a preliminary phylogenetic hypothesis for species in this genus (Hershler, 1994:fig. 31) permitted recognition of several well-supported clades within this group, which may be better treated as separate genera in the future. (Monophyly of *Pyrgulopsis* was not well tested as only a single outgroup was used.) Several additional morphologically cohesive groups are described herein, but allocation of these to new genera is tabled until a more comprehensive phylogenetic review of *Pyrgulopsis* is prepared. Fauna described herein includes not only several distinct, well-delineated groups, some of which may represent local "species flocks" (e.g., in Railroad and Steptoe Valleys), but also a large number of relatively similar yet geographically scattered species of uncertain affinities. Although the latter are contrasted principally on the basis of penial form and ornament, the reader should be aware that characters derived from these features are probably subject to homoplasy and may be misleading with regard to phylogenetic signal. Thus, for instance, it is difficult to confidently ascertain whether some of the new species modestly endowed with glandular ornament on the penis are allied with snails having similar penes or, alternatively, should be interpreted as reduced forms derived from either of two regionally widespread species, *P. gibba* Hershler, 1995, and *P. kolobensis* (Taylor, 1987). Given the large number of species and relatively small number of characters used in the descriptions, it will be difficult to unravel the phylogenetic relationships among these taxa using morphological criteria alone. In any event, such an analysis is beyond the scope of this paper, as it will require additional study of the many other congeners (encompassing characters not utilized in my earlier review) as well as re-evaluation of concepts of character discrimination and state coding based on information derived from the current study.

MATERIALS AND METHODS

This work was principally based on study of material (dry shell and anatomical components) collected during the recent field survey (and now deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.), as other museum material from the region is scarce and almost always of empty shell, which usually cannot be confidently identified to species in this group. Identification of springs to be surveyed was facilitated by study of United States Geological Survey topographic maps (1:100,000 scale) and communications from various colleagues (see Acknowledgments). Mate-

[1] This restricts the Great Basin to the region characterized by internal drainage. Other definitions (physiographic or floristic) outline slightly different regions (see D'Azevedo, 1986:fig. 2).

Table 1

Selected shell parameters for new species of *Pyrgulopsis*. Data expressed as mean with standard deviation given below. Measurements are given in mm. *n* = number of specimens, μ = mean, s = standard deviation, SH = shell height, SW = shell width, HBW = height of body whorl, WBW = width of body whorl, AH = aperture height, AW = aperture width, SS = shell width/shell height, WH = number of shell whorls. In lots marked with an asterisk, the majority of specimens measured had eroded apices.

		SH	SW	HBW	WBW	AH	AW	SS	WH
*P. **fausta***									
USNM 874757	μ	1.56	1.38	1.33	1.11	0.91	0.76	0.88	3.03
n = 15	s	0.07	0.05	0.05	0.03	0.04	0.05	0.03	0.13
*P. **deaconi***									
USNM 874454	μ	1.78	1.49	1.52	1.25	0.98	0.84	0.84	3.18
n = 15	s	0.09	0.07	0.07	0.06	0.06	0.05	0.03	0.11
*P. **coloradensis***									
USNM 854621	μ	1.31	1.13	1.14	0.89	0.74	0.65	0.86	3.17
n = 15	s	0.13	0.08	0.08	0.05	0.05	0.03	0.05	0.25
*P. **montana***									
USNM 874686	μ	2.38	1.79	1.86	1.56	1.17	0.93	0.75	3.51
n = 15	s	0.21	0.11	0.15	0.11	0.08	0.09	0.03	0.26
*P. **hubbsi***									
*USNM 873415	μ	3.14	2.83	2.88	2.22	2.10	1.51	0.90	3.51
n = 15	s	0.25	0.23	0.22	0.18	0.13	0.19	0.03	0.11
USNM 873405	μ	2.82	2.47	2.54	1.89	1.78	1.40	0.88	3.51
n = 15	s	0.21	0.13	0.18	0.12	0.12	0.08	0.03	0.18
*P. **sathos***									
USNM 874464	μ	3.47	2.49	2.67	2.15	1.56	1.32	0.72	4.43
n = 15	s	0.17	0.14	0.16	0.10	0.10	0.07	0.03	0.20
USNM 873198	μ	4.19	3.17	2.97	2.74	1.89	1.54	0.76	4.85
n = 15	s	0.18	0.18	0.13	0.15	0.11	0.10	0.03	0.18
USNM 874663	μ	1.57	1.35	1.19	1.14	0.81	0.66	0.86	3.45
n = 15	s	0.15	0.09	0.10	0.07	0.06	0.06	0.04	0.22
USNM 883852	μ	4.03	3.02	2.94	2.56	1.96	1.52	0.75	4.66
n = 15	s	0.32	0.17	0.21	0.14	0.11	0.13	0.04	0.20
*P. **breviloba***									
USNM 883846	μ	1.67	1.41	1.46	1.10	0.96	0.80	0.85	3.32
n = 10	s	0.12	0.12	0.12	0.08	0.09	0.06	0.05	0.12
USNM 874671	μ	1.28	1.15	1.09	0.92	0.75	0.60	0.87	3.00
n = 15	s	0.07	0.05	0.07	0.05	0.03	0.04	0.03	0.13
USNM 873188	μ	1.69	1.51	1.46	1.11	1.03	0.77	0.89	3.55
n = 15	s	0.11	0.13	0.09	0.08	0.07	0.05	0.05	0.14
*P. **lata***									
USNM 873167	μ	1.95	1.42	1.57	1.22	0.93	0.69	0.73	4.08
n = 15	s	0.08	0.10	0.07	0.06	0.06	0.10	0.04	0.12
*P. **gracilis***									
*USNM 873158	μ	1.71	1.47	1.36	1.26	0.98	0.70	0.86	2.98
n = 12	s	0.08	0.08	0.08	0.06	0.06	0.07	0.04	0.55
*P. **marcida***									
USNM 873154	μ	3.41	2.63	2.48	2.18	1.64	1.31	0.77	4.15
n = 15	s	0.17	0.15	0.16	0.11	0.09	0.11	0.03	0.21
USNM 873170	μ	2.73	1.94	2.06	1.68	1.26	0.98	0.71	4.22
n = 15	s	0.15	0.08	0.10	0.08	0.04	0.05	0.03	0.23
*USNM 874672	μ	1.79	1.41	1.47	1.20	0.98	0.77	0.79	3.52
n = 15	s	0.13	0.07	0.10	0.06	0.08	0.05	0.04	0.15
USNM 874682	μ	3.12	2.45	2.39	2.09	1.59	1.25	0.77	3.75
n = 15	s	0.22	0.18	0.14	0.11	0.10	0.09	0.03	0.16

Table 1

Continued.

		SH	SW	HBW	WBW	AH	AW	SS	WH
P. turbatrix									
USNM 883978	μ	3.08	1.96	2.22	1.65	1.26	1.15	0.64	4.45
n = 15	s	0.15	0.07	0.10	0.06	0.07	0.05	0.03	0.17
USNM 857936	μ	2.28	1.60	1.77	1.38	1.06	0.94	0.70	3.82
n = 15	s	0.11	0.05	0.07	0.04	0.05	0.04	0.03	0.15
USNM 883550	μ	3.22	2.00	2.20	1.75	1.24	1.04	0.62	4.67
n = 13	s	0.20	0.09	0.11	0.08	0.06	0.06	0.03	0.19
USNM 883981	μ	2.51	1.80	1.88	1.52	1.12	1.01	0.72	4.00
n = 15	s	0.15	0.13	0.11	0.07	0.09	0.06	0.02	0.21
P. sterilis									
USNM 874876	μ	3.51	2.41	2.49	2.06	1.56	1.26	0.69	4.30
n = 15	s	0.19	0.09	0.15	0.07	0.10	0.06	0.03	0.22
USNM 874679	μ	2.52	2.00	2.05	1.60	1.30	1.15	0.80	3.43
n = 15	s	0.16	0.11	0.10	0.11	0.09	0.06	0.02	0.18
P. ruinosa									
USNM 873407	μ	2.91	2.08	2.25	1.83	1.35	1.05	0.72	4.02
n = 15	s	0.19	0.14	0.14	0.11	0.10	0.08	0.05	0.22
P. sublata									
USNM 874681	μ	2.42	1.73	1.81	1.56	1.12	0.91	0.72	4.18
n = 15	s	0.18	0.14	0.12	0.12	0.08	0.08	0.03	0.20
P. lockensis									
USNM 874779	μ	1.79	1.53	1.37	1.27	0.89	0.80	0.86	3.50
n = 15	s	0.08	0.05	0.05	0.04	0.04	0.03	0.03	0.21
P. papillata									
USNM 873185	μ	2.04	1.76	1.62	1.45	1.10	0.99	0.87	3.43
n = 15	s	0.10	0.06	0.07	0.06	0.06	0.05	0.04	0.15
P. carinata									
USNM 883975	μ	2.10	1.77	1.67	1.47	1.09	0.91	0.85	3.71
n = 12	s	0.22	0.14	0.16	0.11	0.07	0.09	0.03	0.21
P. aloba									
*USNM 883847	μ	1.18	1.04	1.03	0.86	0.68	0.57	0.89	2.42
n = 12	s	0.08	0.06	0.07	0.05	0.06	0.04	0.05	0.27
USNM 873187	μ	1.30	1.19	1.14	0.97	0.79	0.65	0.92	3.10
n = 15	s	0.16	0.13	0.12	0.11	0.09	0.07	0.03	0.18
P. villacampae									
USNM 873191	μ	2.82	2.52	2.47	2.00	1.62	1.53	0.90	3.37
n = 15	s	0.14	0.10	0.15	0.07	0.10	0.09	0.04	0.16
USNM 883938	μ	3.37	2.87	2.78	2.27	1.86	1.69	0.85	3.81
n = 12	s	0.21	0.14	0.20	0.10	0.13	0.11	0.03	0.19
P. anatina									
USNM 883848	μ	2.66	2.01	1.95	1.71	1.28	1.04	0.76	4.00
n = 15	s	0.13	0.11	0.10	0.07	0.07	0.06	0.03	0.19
P. planulata									
*USNM 892023	μ	1.30	1.29	1.26	1.15	0.80	0.72	1.00	2.01
n = 15	s	0.06	0.08	0.07	0.06	0.06	0.05	0.05	0.24
P. sulcata									
USNM 874326	μ	1.31	1.11	1.05	0.96	0.71	0.56	0.85	3.80
n = 15	s	0.06	0.03	0.04	0.04	0.03	0.03	0.03	0.17
P. orbiculata									
USNM 873196	μ	1.28	1.13	1.08	0.97	0.70	0.60	0.88	3.53
n = 15	s	0.05	0.04	0.04	0.02	0.02	0.03	0.04	0.19
P. neritella									
*USNM 883932	μ	1.45	1.35	1.40	1.03	0.99	0.91	0.93	2.30
n = 15	s	0.08	0.05	0.11	0.05	0.06	0.06	0.05	0.40

Table 1

Continued.

		SH	SW	HBW	WBW	AH	AW	SS	WH
*USNM 883936	μ	1.33	1.08	1.32	1.05	0.86	0.75	0.82	1.62
n = 15	s	0.08	0.05	0.08	0.05	0.06	0.06	0.03	0.21
P. landyei									
*USNM 892014	μ	1.41	1.25	1.25	1.12	0.78	0.68	0.89	3.02
n = 15	s	0.08	0.07	0.06	0.04	0.06	0.05	0.03	0.35
P. serrata									
USNM 874314	μ	2.22	1.73	1.75	1.49	1.05	0.93	0.78	3.73
n = 15	s	0.11	0.09	0.09	0.06	0.06	0.05	0.05	0.18
*USNM 874312	μ	3.54	2.30	2.33	2.09	1.35	1.15	0.65	4.48
n = 13	s	0.30	0.13	0.14	0.12	0.09	0.07	0.04	0.45
USNM 874318	μ	2.32	1.73	1.78	1.49	1.09	0.96	0.75	3.93
n = 15	s	0.15	0.10	0.10	0.08	0.09	0.06	0.05	0.15
P. cruciglans									
USNM 874285	μ	1.78	1.40	1.41	1.19	0.89	0.75	0.79	3.80
n = 15	s	0.10	0.04	0.06	0.05	0.03	0.03	0.03	0.17
USNM 874327	μ	2.39	1.88	1.93	1.57	1.20	1.06	0.79	3.87
n = 15	s	0.13	0.08	0.10	0.08	0.06	0.05	0.04	0.18
USNM 874331	μ	2.33	1.84	1.83	1.53	1.13	0.98	0.79	3.90
n = 15	s	0.13	0.08	0.08	0.06	0.07	0.06	0.04	0.16
USNM 874335	μ	2.33	1.86	1.85	1.57	1.20	0.98	0.80	3.92
n = 15	s	0.19	0.13	0.13	0.11	0.08	0.07	0.04	0.15
P. dixensis									
USNM 874391	μ	1.78	0.91	1.08	0.86	0.62	0.50	0.52	4.82
n = 15	s	0.10	0.03	0.06	0.04	0.04	0.03	0.02	0.24
P. aurata									
USNM 874393	μ	2.69	2.14	2.19	1.70	1.37	1.18	0.80	3.92
n = 15	s	0.13	0.09	0.11	0.07	0.08	0.06	0.02	0.18
P. longiglans									
USNM 873409	μ	2.41	1.81	1.92	1.52	1.27	1.02	0.76	3.90
n = 15	s	0.08	0.05	0.06	0.04	0.03	0.03	0.03	0.13
USNM 874288	μ	1.54	1.27	1.27	1.06	0.85	0.62	0.82	3.45
n = 15	s	0.10	0.06	0.07	0.06	0.04	0.03	0.02	0.17
USNM 883486	μ	1.97	1.58	1.57	1.32	1.03	0.77	0.80	3.93
n = 15	s	0.08	0.09	0.06	0.05	0.05	0.05	0.03	0.11
USNM 874293	μ	1.93	1.55	1.60	1.27	1.10	0.80	0.80	3.67
n = 15	s	0.16	0.10	0.11	0.07	0.08	0.06	0.04	0.18
USNM 874396	μ	2.10	1.59	1.69	1.34	1.12	0.85	0.76	3.87
n = 15	s	0.10	0.06	0.08	0.04	0.04	0.05	0.03	0.16
USNM 874904	μ	1.79	1.41	1.44	1.18	0.96	0.69	0.79	3.82
n = 15	s	0.11	0.06	0.08	0.05	0.05	0.03	0.03	0.20
P. militaris									
USNM 873203	μ	1.44	1.23	1.23	0.96	0.83	0.65	0.85	3.52
n = 15	s	0.08	0.05	0.06	0.04	0.05	0.04	0.03	0.11
USNM 883921	μ	1.75	1.46	1.46	1.17	0.93	0.76	0.83	3.48
n = 15	s	0.10	0.06	0.08	0.05	0.05	0.03	0.04	0.15
P. umbilicata									
USNM 873208	μ	2.13	1.74	1.71	1.49	1.05	0.89	0.82	3.80
n = 15	s	0.08	0.07	0.07	0.07	0.05	0.05	0.02	0.10
USNM 873202	μ	1.87	1.59	1.53	1.32	1.02	0.82	0.85	3.72
n = 15	s	0.11	0.08	0.08	0.06	0.05	0.04	0.03	0.16
P. limaria									
USNM 873232	μ	1.55	1.41	1.31	1.14	0.90	0.71	0.91	3.45
n = 15	s	0.10	0.06	0.08	0.06	0.04	0.04	0.04	0.14

Table 1

Continued.

		SH	SW	HBW	WBW	AH	AW	SS	WH
P. notidicola									
USNM 873215	μ	2.22	1.83	1.95	1.45	1.25	1.07	0.82	3.47
n = 15	s	0.09	0.08	0.08	0.06	0.04	0.04	0.04	0.14
USNM 874286	μ	1.56	1.40	1.37	1.05	0.93	0.79	0.89	3.18
n = 15	s	0.13	0.10	0.11	0.07	0.06	0.06	0.03	0.15
USNM 874294	μ	1.78	1.50	1.57	1.20	0.99	0.88	0.84	3.30
n = 15	s	0.07	0.07	0.07	0.05	0.05	0.06	0.03	0.10
P. vinyardi									
USNM 874740	μ	1.72	1.45	1.54	1.17	0.98	0.86	0.84	3.25
n = 14	s	0.11	0.08	0.09	0.06	0.05	0.06	0.04	0.14
P. imperialis									
USNM 874207	μ	1.53	1.12	1.21	0.95	0.76	0.58	0.73	3.43
n = 15	s	0.07	0.06	0.05	0.04	0.03	0.04	0.04	0.18
USNM 874211	μ	1.59	1.17	1.26	1.00	0.78	0.60	0.74	3.45
n = 15	s	0.09	0.07	0.06	0.04	0.04	0.04	0.04	0.17
P. sadai									
USNM 874397	μ	2.68	2.07	2.17	1.75	1.37	1.08	0.77	4.17
n = 15	s	0.09	0.09	0.08	0.06	0.05	0.08	0.02	0.11
USNM 874208	μ	2.31	1.86	1.87	1.57	1.21	0.98	0.81	3.88
n = 15	s	0.13	0.08	0.11	0.09	0.05	0.06	0.03	0.13
USNM 874388	μ	2.20	1.84	1.84	1.56	1.20	0.99	0.84	3.58
n = 15	s	0.17	0.11	0.12	0.09	0.07	0.06	0.02	0.20
USNM 874392	μ	2.38	1.78	1.85	1.55	1.14	0.99	0.75	3.87
n = 15	s	0.19	0.10	0.12	0.09	0.07	0.06	0.03	0.19
USNM 883900	μ	2.92	2.16	2.25	1.91	1.36	1.12	0.74	4.13
n = 15	s	0.16	0.07	0.09	0.07	0.04	0.04	0.04	0.13
P. augustae									
USNM 874402	μ	2.32	1.45	1.71	1.26	1.07	0.77	0.63	4.25
n = 14	s	0.10	0.07	0.08	0.06	0.05	0.04	0.02	0.24
P. pictilis									
USNM 874401	μ	2.35	1.88	1.94	1.58	1.26	1.01	0.81	3.80
n = 15	s	0.20	0.13	0.15	0.10	0.08	0.07	0.03	0.19
P. basiglans									
USNM 874280	μ	1.46	1.20	1.18	1.06	0.68	0.62	0.82	3.45
n = 15	s	0.13	0.05	0.08	0.07	0.04	0.04	0.04	0.24
P. bifurcata									
USNM 874306	μ	1.50	1.16	1.14	1.01	0.68	0.62	0.78	3.67
n = 15	s	0.11	0.06	0.07	0.06	0.05	0.04	0.04	0.18
P. pellita									
USNM 883850	μ	2.49	1.93	2.00	1.66	1.28	1.04	0.78	3.67
n = 15	s	0.17	0.09	0.13	0.08	0.07	0.06	0.04	0.23
P. leporina									
USNM 874336	μ	3.61	2.57	2.70	2.26	1.65	1.38	0.71	4.07
n = 14	s	0.27	0.18	0.16	0.18	0.10	0.08	0.04	0.45
P. humboldtensis									
USNM 874722	μ	2.23	1.87	1.88	1.55	1.18	0.99	0.84	3.53
n = 15	s	0.10	0.09	0.07	0.06	0.05	0.06	0.03	0.16
USNM 874719	μ	2.72	2.10	2.19	1.79	1.33	1.17	0.77	3.78
n = 15	s	0.15	0.09	0.11	0.07	0.06	0.06	0.03	0.16
USNM 874725	μ	2.58	2.16	2.15	1.73	1.38	1.20	0.84	3.77
n = 15	s	0.12	0.14	0.12	0.10	0.08	0.08	0.04	0.16
P. hamlinensis									
USNM 883215	μ	1.84	1.15	1.29	1.07	0.73	0.59	0.63	4.13
n = 15	s	0.11	0.05	0.06	0.05	0.03	0.04	0.03	0.21

Table 1

Continued.

		SH	SW	HBW	WBW	AH	AW	SS	WH
P. peculiaris									
*USNM 883933	μ	2.19	1.74	1.83	1.48	1.13	0.97	0.80	3.55
n = 15	s	0.09	0.07	0.10	0.05	0.06	0.05	0.03	0.22
USNM 874683	μ	2.13	1.43	1.61	1.30	0.95	0.80	0.67	4.17
n = 15	s	0.14	0.07	0.07	0.05	0.05	0.05	0.03	0.15
USNM 883222	μ	1.84	1.52	1.62	1.26	1.03	0.90	0.83	3.33
n = 15	s	0.07	0.05	0.05	0.04	0.03	0.04	0.03	0.24
USNM 883227	μ	2.33	1.75	1.93	1.51	1.16	1.01	0.75	3.93
n = 15	s	0.10	0.10	0.10	0.07	0.09	0.08	0.02	0.15
USNM 883622	μ	2.77	2.02	2.19	1.72	1.26	1.16	0.73	4.21
n = 15	s	0.11	0.07	0.07	0.06	0.05	0.04	0.02	0.16
USNM 883603	μ	2.52	1.90	2.03	1.60	1.22	1.08	0.76	3.98
n = 15	s	0.15	0.09	0.10	0.06	0.08	0.05	0.02	0.18
P. anguina									
*USNM 874678	μ	2.20	1.95	1.93	1.60	1.31	1.08	0.89	3.02
n = 15	s	0.13	0.13	0.14	0.08	0.12	0.07	0.03	0.68
USNM 883205	μ	2.77	2.12	2.22	1.79	1.39	1.14	0.77	4.15
n = 15	s	0.23	0.14	0.18	0.14	0.09	0.09	0.03	0.21
P. saxatilis									
USNM 883237	μ	1.16	1.11	1.04	0.83	0.80	0.62	0.96	3.23
n = 15	s	0.10	0.08	0.09	0.07	0.05	0.05	0.04	0.20
P. variegata									
USNM 883627	μ	2.45	1.69	1.95	1.49	1.14	0.92	0.69	3.96
n = 15	s	0.12	0.07	0.09	0.08	0.05	0.04	0.03	0.13
USNM 883888	μ	2.69	1.86	2.08	1.60	1.26	1.02	0.69	4.10
n = 15	s	0.12	0.10	0.11	0.09	0.08	0.08	0.03	0.16
USNM 874713	μ	2.76	1.98	2.21	1.66	1.36	1.10	0.72	4.05
n = 15	s	0.10	0.07	0.08	0.05	0.05	0.06	0.02	0.17
USNM 883599	μ	3.11	2.11	2.44	1.78	1.44	1.18	0.68	4.30
n = 15	s	0.15	0.13	0.12	0.08	0.08	0.09	0.04	0.19
USNM 883614	μ	2.98	2.16	2.38	1.80	1.45	1.24	0.73	3.95
n = 15	s	0.14	0.10	0.13	0.09	0.11	0.08	0.03	0.19
*USNM 883624	μ	2.46	1.79	1.98	1.53	1.21	1.02	0.73	3.85
n = 15	s	0.17	0.13	0.15	0.10	0.11	0.09	0.02	0.16
USNM 883583	μ	2.31	1.70	1.82	1.41	1.14	0.96	0.73	3.95
n = 15	s	0.13	0.10	0.10	0.07	0.05	0.06	0.03	0.10
USNM 874721	μ	2.34	1.73	1.86	1.48	1.15	0.96	0.74	3.85
n = 15	s	0.12	0.09	0.08	0.07	0.05	0.04	0.02	0.13
P. hovinghi									
USNM 874075	μ	2.43	1.85	1.95	1.58	1.19	1.01	0.76	3.88
n = 15	s	0.13	0.07	0.08	0.06	0.04	0.07	0.03	0.21
P. millenaria									
USNM 874720	μ	2.70	1.98	2.15	1.70	1.38	1.10	0.73	3.92
n = 15	s	0.16	0.13	0.12	0.06	0.10	0.08	0.03	0.18
P. lentiglans									
USNM 874724	μ	1.63	1.09	1.15	0.99	0.71	0.56	0.67	4.05
n = 15	s	0.10	0.07	0.08	0.05	0.04	0.05	0.03	0.14
USNM 854540	μ	1.49	0.92	1.04	0.86	0.57	0.45	0.62	3.93
n = 15	s	0.05	0.02	0.03	0.02	0.02	0.02	0.02	0.11
P. plicata									
USNM 883594	μ	2.59	1.99	2.18	1.63	1.34	1.11	0.77	3.90
n = 15	s	0.17	0.12	0.16	0.08	0.10	0.07	0.03	0.16

Table 1

Continued.

		SH	SW	HBW	WBW	AH	AW	SS	WH
P. fusca									
USNM 883439	μ	2.86	1.99	2.18	1.74	1.33	1.08	0.70	4.05
n = 15	s	0.18	0.11	0.13	0.09	0.12	0.06	0.03	0.19
USNM 883573	μ	3.50	2.37	2.64	2.06	1.56	1.29	0.68	4.33
n = 13	s	0.37	0.20	0.28	0.18	0.15	0.12	0.04	0.26
P. chamberlini									
USNM 854786	μ	2.83	1.96	2.16	1.74	1.24	1.16	0.69	4.33
n = 15	s	0.18	0.13	0.14	0.10	0.09	0.09	0.04	0.18
USNM 854784	μ	4.05	2.88	3.13	2.43	1.91	1.54	0.71	4.82
n = 15	s	0.31	0.15	0.24	0.13	0.14	0.13	0.03	0.20
P. inopinata									
USNM 854783	μ	3.27	1.98	2.26	1.79	1.25	1.03	0.61	4.75
n = 15	s	0.12	0.07	0.09	0.09	0.05	0.06	0.03	0.16
USNM 854785	μ	2.45	1.52	1.74	1.41	0.95	0.79	0.62	4.29
n = 13	s	0.12	0.09	0.10	0.08	0.05	0.06	0.02	0.14
P. nonaria									
USNM 883566	μ	2.66	1.71	1.98	1.55	1.17	0.90	0.65	4.13
n = 15	s	0.11	0.09	0.06	0.05	0.06	0.07	0.03	0.16
P. transversa									
USNM 883221	μ	2.15	1.50	1.68	1.28	1.27	0.95	0.69	3.93
n = 15	s	0.15	0.12	0.09	0.09	0.10	0.09	0.03	0.15
USNM 883422	μ	2.79	1.81	2.11	1.57	1.27	0.98	0.65	4.40
n = 15	s	0.12	0.07	0.11	0.05	0.05	0.05	0.02	0.18
USNM 883210	μ	2.71	1.91	2.14	1.66	1.26	1.08	0.71	4.15
n = 15	s	0.11	0.11	0.09	0.06	0.06	0.05	0.04	0.18
USNM 883481	μ	2.49	1.71	1.99	1.47	1.27	0.95	0.69	3.93
n = 15	s	0.21	0.12	0.16	0.09	0.10	0.09	0.03	0.15
USNM 883597	μ	2.99	2.10	2.33	1.76	1.41	1.16	0.70	4.32
n = 15	s	0.12	0.07	0.11	0.06	0.08	0.08	0.02	0.20
USNM 883572	μ	2.70	1.87	2.07	1.66	1.25	1.01	0.69	3.97
n = 15	s	0.19	0.11	0.11	0.09	0.08	0.06	0.03	0.19

rial was collected during the course of the field survey by washing stones or sweeping soft sediment or aquatic vegetation with a small hand sieve. Samples were placed in glass jars, narcotized with crushed menthol crystals for about 13 hours, fixed in dilute (4%) formalin, and then preserved in 70% ethanol. Legal coordinates and land ownership status were noted for each site (from 1:100,000 topographic maps), as were elevation and a variety of habitat data. Distribution maps were prepared from spatial databases obtained from the United States Geological Survey digital line graph (for drainage and political boundaries). Locations of snail-positive sites were digitized from the 1:100,000 maps. Mapping data were processed in Arc/Info with dBase5.0.

Institutional repositories of examined specimens are indicated by the following abbreviations: FMNH, Field Museum of Natural History, Chicago; SBMNH, Santa Barbara Museum of Natural History; UCM, University of Colorado Museum, Boulder; UMMZ, University of Michigan Museum of Zoology, Ann Arbor; USNM, former United States National Museum, collections now in National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Shell parameters were obtained from one or more randomly selected samples of about 15 adult specimens (as indicated by completion of the inner shell lip) for each new species using methods of Hershler (1989). Descriptive statistics for these parameters were generated using SYSTAT (Wilkinson, 1986) and are summarized in Table 1. Shells, opercula, and radulae were cleansed in commercial bleach (CLOROX), rinsed in distilled water, mounted on stubs, and then studied and photographed using a Leica 440 Scanning Electron Microscope (SEM).

Body pigmentation was studied for alcohol-preserved material and, although most of this material was recently collected, color has probably faded in older lots. Anatomical study was of specimens soaked in Bouin's Solution to remove inorganic shell material. Animals were dissected in dilute Bouin's Solution using methods of Hershler (1994:2). Crude sections of female capsule gland

and male prostate gland were cut using iridectomy scissors. Anatomical illustrations were prepared from camera lucida drawings. Five or six specimens of each sex (paratypes or topotypes) were usually dissected for each species, although additional series were added for species that are either widely distributed or show significant geographic variation in shell features. For description of penial variation, a series of 10–30 penes was excised and studied from all available samples for each species. Terminology of penial morphology and glands is that of Hershler (1994:5–6; also see Figure 26).

The following morphologic features were scrutinized when preparing species descriptions:

Shell: shape, height, width, number of whorls, number of protoconch whorls, protoconch diameter, protoconch sculpture, shape of teleoconch whorls, aperture shape, relationship between inner lip and body whorl, thickness of lip, width of columellar shelf, shape and inclination of outer lip, umbilicus development, periostracum color.

Operculum: shape, color, number of whorls, location of nucleus, frilling of whorl outlines on dorsal surface, development of rim along outer margin, thickening of attachment scar margin.

Digestive system: length and width of radular ribbon, number of tooth rows; width, dorsal indentation, number of lateral cusps, shape of central cusp, size of basal cusps, shape of basal tongue, depth of basal sockets on central radular teeth; tooth formula, flexure of neck, length of outer wing relative to cutting edge of lateral radular teeth; number of cusps, length of cutting edge relative to overall length of inner and outer marginal teeth; length of stomach relative to style sac, relative sizes of anterior and posterior stomach chambers, size of stomach caecum.

Body pigmentation: color, intensity, location of pigmentation on cephalic tentacles, snout, foot, opercular lobe, neck, pallial roof, visceral coil, penis.

Pallial cavity: number of ctenidial filaments, presence of pleats on filaments, posterior extent of ctenidium; osphradium size, shape and position relative to ctenidial axis; orientation of renal gland, thickening of kidney opening, extent to which rectum overlaps genital ducts.

Female animal: number of whorls occupied by ovary, length of ovary relative to digestive gland behind stomach, anterior extension of ovary, extent of pallial portion of albumen gland relative to overall length of gland, relative lengths of albumen and capsule glands, shape of capsule gland in section, development of rectal furrow on capsule gland, extent to which ventral channel overlaps capsule gland, development of longitudinal fold of ventral channel; shape, position, and anterior extension of genital aperture; shape and number of oviduct coils, position of junction of oviduct and bursal duct, length and width of bursa copulatrix relative to albumen gland; shape, orientation relative to albumen gland, posterior extent of bursa copulatrix; origin, length and width (relative to bursa copulatrix) of bursal duct; position of bursal duct relative to surface of albumen gland; size (relative to length of bursa copulatrix), shape, position of seminal receptacle.

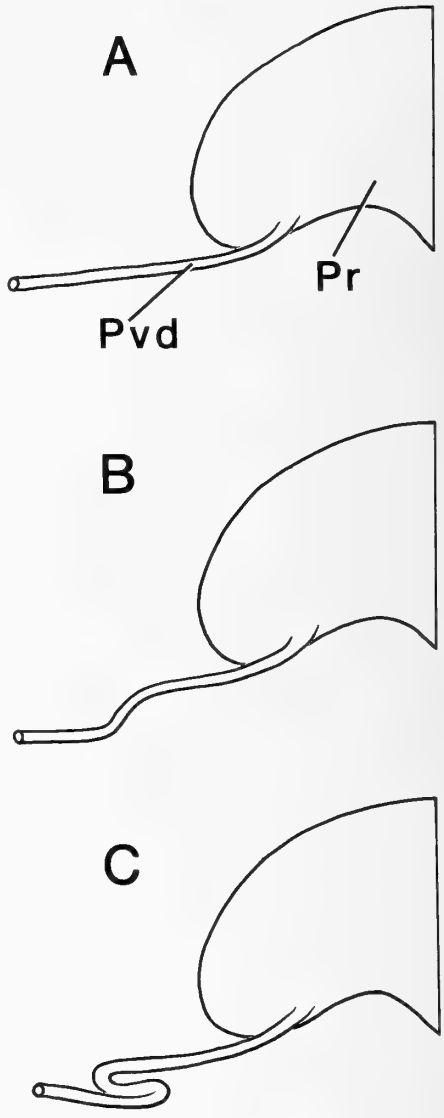


Figure 2

Schematic diagram of the anterior portion of the prostate gland (viewed from the left side) showing variation in coiling of the pallial vas deferens. A. Vas deferens straight. B. With weak undulation. C. With prominent, reflexed bend. Pr = prostate gland, Pvd = pallial vas deferens.

Male animal: number of whorls occupied by testis, length of testis relative to digestive gland behind stomach, anterior extension of testis; size, shape of prostate gland, extent of pallial portion of prostate gland, shape of prostate gland in section; shape of proximal portion of pallial vas deferens (Figure 2); size of penis relative to head; shape and folding of base of penis; length (relative to base), width, shape, orientation of filament and lobe;

Figure 3

Representative Great Basin springs. A. Horseshutem Springs, nestled along the western flank of the Spring Mountains (1480 m elevation) in southeast Nevada. This small rheocrene, severely impacted by cattle, is the type locality of *P.* ***turbatrix.*** Photograph by D. Sada, July, 1995. B. One of many small, thermal rheocrenes in the Mud Meadow drainage in northwest Nevada. Water temperature at this site was 39°C. and *P.* ***notidicola*** was found living in a moistened zone just outside the water. Note the artificial impoundment and old gauge box at the source of this spring. Photograph by G. Vinyard, August, 1991. C. Unnamed spring in Park Valley, northwest Utah. One of many highly mineralized springs in the Bonneville Basin inhabited by *P. kolobensis.* Photograph, August, 1993. D. Unnamed springs in the Simpson Mountains (1779 m elevation), overlooking the Old River Bed in southern Utah. These small, mineralized (1126 micromhos/cm) rheocrenes compose the type locality of *P.* ***transversa.*** Photograph, May, 1993.

number, size, position, orientation, apparent fusion of glands on penis; shape, position of penial duct.

Previously described species are treated only when new records were obtained from the field survey. Literature compilations pertaining to these snails are in Taylor (1975) and my recent review of *Pyrgulopsis* (Hershler, 1994). Synonomies for these taxa are not intended to be complete, but instead detail original citation of species (and synonyms), assignment to *Pyrgulopsis,* treatments of material from the study area, and pertinent references to the broader works listed above. A common name is proposed for each new species to facilitate their reference by governmental agencies.

NATURAL HISTORY

Pyrgulopsis are widespread within the Great Basin where they occur in a variety of relatively small, usually fishless, spring-fed water bodies (Figures 3–5). These animals also historically occurred in a few of the Great Basin lakes, with the main example provided by *P. nevadensis* (Stearns, 1883), which lived in Pyramid Lake (of the Lahontan Basin) until becoming extinct around the turn of the century. Members of this genus have not been found in any of the rivers of the Great Basin. The most common habitat for these snails is a rheocrene, or a spring which emerges from the ground as a flowing stream. *Pyrgulopsis* also occur in limnocrenes, in which the headspring forms a natural pool (which is drained by a flowing stream), and helocrenes, springs that comprise marshlike situations. Waters harboring *Pyrgulopsis* range from small seeps with miniscule discharge and depth of 1 cm or less, to large springs such as those feeding Clear Lake in southern Utah, whose discharge is about 6.8 m^3/sec (Mundorff, 1971:62). While most of these springs are of medium temperature (e.g., 10–21°C.), snails were also found in more than 50 thermal springs (e.g., those having temperature greater than 21°C.; per Garside & Schilling, 1979:1). While most of these springs were in the 22–35° range, it is worth noting that in the two cases in which even warmer (ca. 39°C.) water was involved (i.e., springs in Mud Meadows harboring *P.* **notidicola**; described below), most of the snails seen were madicolous, inhabiting a moistened zone around the margins of the spring. While most of the springs were of low to medium conductivity (e.g., 200–600 micromhos/cm), *Pyrgulopsis* were collected from more than 50 brackish springs (having greater than 1 gm/1 total dissolved solids; Todd, 1980), most of which were along the margins of the Great Salt Lake Desert (and harbored *P. kolobensis*).

Pyrgulopsis often decline dramatically in density downflow from spring sources, presumably reflecting their requirement for the well-known stable temperature, chemistry, and flow regime characterizing headsprings (Deacon & Minckley, 1974). This pattern of distribution is most pronounced in smaller springs, while in larger habitats *Pyrgulopsis* may occur far downstream from spring sources.

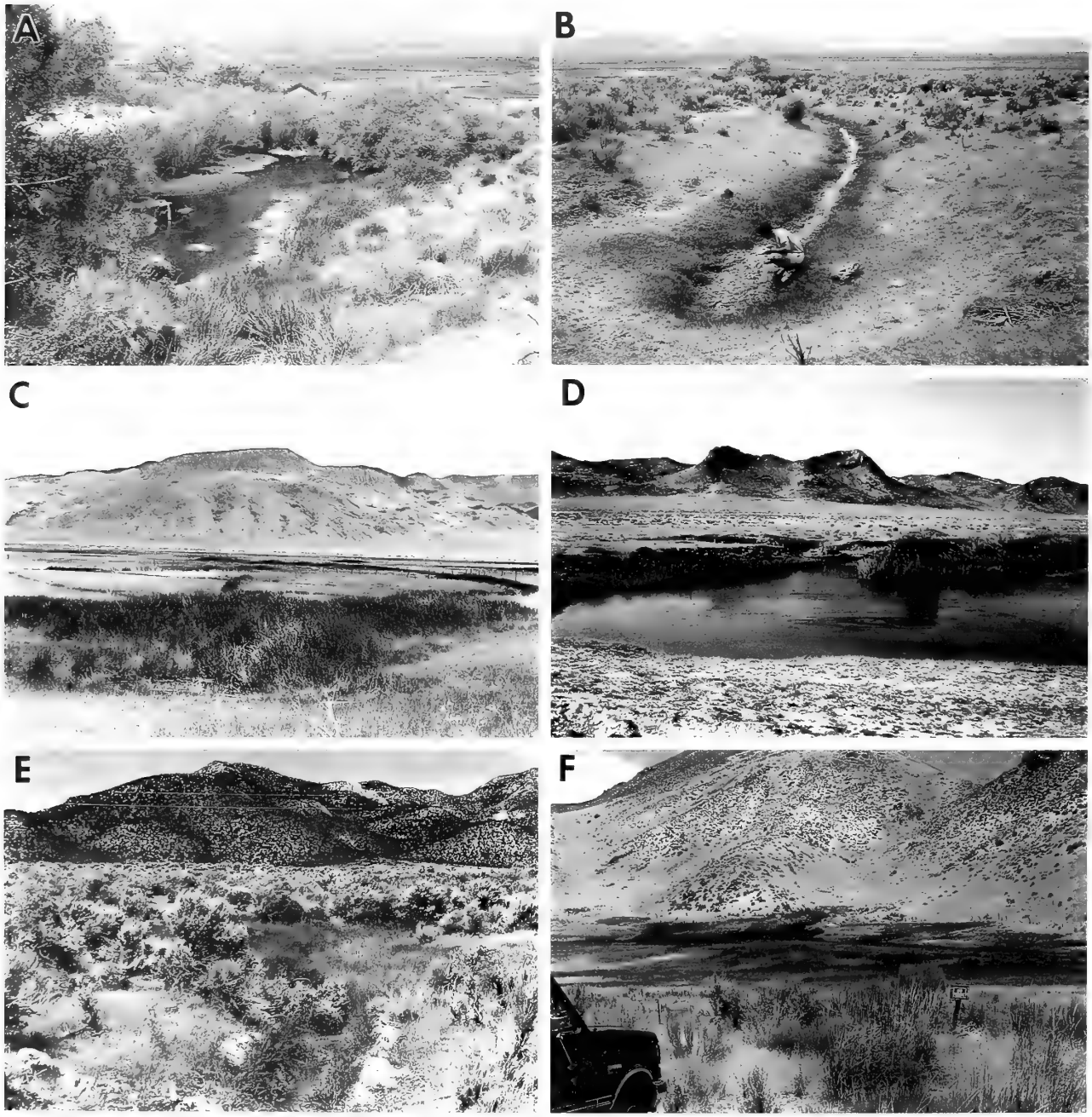


Figure 4

Representative Great Basin springs. A. The northernmost spring in the Flag Spring complex, White River Valley, Nevada. This limnocrene (pool diameter about 15 m) is the type locality of *P.* ***sathos,*** which was collected along the margins of the 14 m diameter pool. *Pyrgulopsis* ***breviloba*** was abundant in the outflow channel below the pool. Photograph, June 1992. B. The southernmost spring in the Emigrant Springs complex, White River Valley, Nevada. *Pyrgulopsis* ***gracilis*** and *P.* ***marcida*** co-occur in this small rheocrene, which is highly impacted by cattle. Photograph, June 1992. C. Unnamed basin floor spring in Fish Lake Valley, Nevada. The source of this spring is a small (2 m diameter), thermal (26°C.) limnocrene. The narrow outflow is the type locality of *P.* ***ruinosa,*** now believed to be extinct. Photograph, July 1988. D. Big Warm Spring, a large, thermal (30.5°C.) limnocrene in Duckwater Valley, Nevada. This is the type locality of *P.* ***papillata,*** and *P.* ***villacampae*** also is present. Photograph, D. Sada, October 1992. E. One of many small rheocrenes that compose a large wetland along the southeastern edge of Steptoe Valley near Ely, Nevada, which contains a series of locally endemic snail species (as well as *P. kolobensis*). This site is the type locality of *P.* ***sulcata.*** Photograph, August 1991. F. Series of small rheocrenes along Pine Creek, Humboldt River drainage, Nevada, which harbor *P. gibba.* Photograph, July 1991.

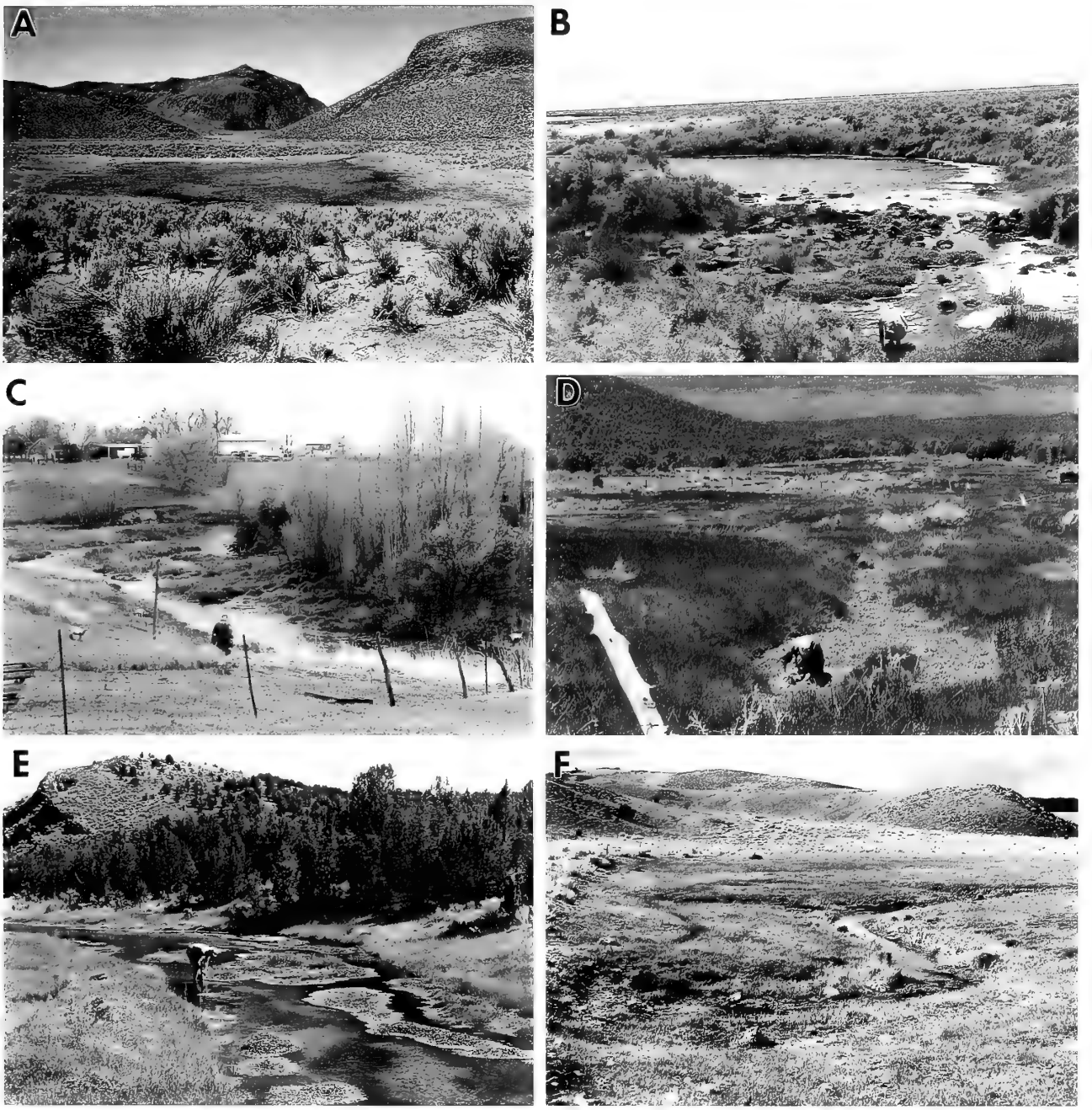


Figure 5

Representative Great Basin springs. A. Wetland fed by a series of small, mineralized (ca. 1000 micromhos/cm) springs, perched in the Shoshone Range above Reese River Valley, Nevada. This is the type locality of *P.* ***sadai,*** which was found in only one of these springs (in a small area of about 1 m^2), all of which were highly degraded by cattle. Photograph, July 1994. B. Bar M Spring, one of the many brackish springs along the northern edge of the Great Salt Lake (Utah) that harbors *P. kolobensis.* Photograph, July 1993. C. Salt Spring, another brackish spring in northern Utah harboring *P. kolobensis.* Photograph, May 1993. D. Unnamed springs along the eastern flank of the White Rock Mountains (2180 m elevation), overlooking Hamlin Valley, Utah. This is the type locality of *P.* ***hamlinensis,*** which occurred abundantly in the dense stand of watercress lining the small stream. Photograph, May 1993. E. Broad (8 m), shallow, spring-fed stream tributary to Etna Reservoir, Grouse Creek Valley, Utah, harboring *P.* ***variegata.*** Photograph, July 1993. F. Series of small rheocrenes, Thousand Springs Creek drainage, Nevada, comprising the type locality of *P.* ***millenaria.*** Photograph, August 1992.

Pyrgulopsis are most commonly found among aquatic vegetation, especially Cress (*Rorippa*[2]), which often forms dense mats lining outflows of small springs. In larger limnocrenes (which often are thermal), snails may be found on other aquatic plants such as Bladderwort (*Utricularia*), or on the bases of riparian Spike rush (*Eleocharis*) or Tule (*Scirpus*). Snails are also often found on hard substrates such as bedrock or pieces of travertine. *Pyrgulopsis* are rarely found on or in soft sediment. Although quantitative sampling of snails was not pursued during this project, the densities of 1000–10,000 snails/m^2 reported for several limnocrene springs in eastern Nevada by Deacon et al. (1980) are probably typical for that habitat in the Great Basin, and considerably less than those of snails inhabiting the smaller rheocrenes. As an indication of the typical local abundance of these animals, a few minutes of sampling at a site usually yielded several hundred living individuals.

Pyrgulopsis are not only found in basin floor springs, which often line the perimeter of dry lake beds and whose outflows coalesce to form large marshes, but also in springs farther up the mountain slopes as well as in spring brooks and streams coursing along well-defined canyons. The snails were collected from sites ranging up to about 2440 m elevation, but appeared to "drop out" in higher alpine situations. For the most part, members of this fauna are distributed in an allopatric fashion. Sympatry of two (and rarely three) congeners was documented at only 14 of the more than 400 sites listed herein, most of which were springs in Duckwater and Steptoe Valley where series of locally endemic species occur. Although the fauna includes several widespread species, notably *P. gibba* and *P. kolobensis,* local endemism is a more common feature. Note that 22 of the 58 new species appear to be restricted to single localities. Details of biology have not been studied for *Pyrgulopsis* of the Great Basin. In the sole detailed study of biology of any species of the genus, Mladenka (1992) determined that *P. bruneauensis,* which is endemic to thermal springs in the Snake River drainage of southern Idaho, is a non-selective grazer of algae and diatoms. As with other congeners, the Great Basin species are oviparous, with females depositing single, small egg capsules on hard substrates.

Two of the species described herein (*P.* ***carinata*** and *P.* ***ruinosa***) apparently have become extinct during the past one or two decades. Relatively few of the collecting sites are in pristine condition, with livestock grazing being the predominant source of disturbance. Smaller, basin floor springs in particular were often profoundly disturbed by cattle, which modify the habitat both physically and chemically by trampling, removing aquatic and riparian vegetation, and depositing urine and feces. The resulting habitat often is largely unsuitable for *Pyrgulopsis,* although snails may persist in a small, upflow "refuge" of clean, flowing water which cows cannot reach. Additional, but less prevalent sources of disturbance are related to human residential and recreational activities, notably diversion and/or withdrawal of water. Exotic biota also may pose a serious threat to these populations, particularly crayfish, which have been widely introduced into the region's waters (Bouchard, 1978; Johnson, 1986) and, although omnivorous, often feed on small gastropods (Covich, 1978; Vermeij & Covich, 1978). An Asiatic gastropod, *Melanoides tuberculata* (Müller, 1774), now thrives in many of the warm springs of the Great Basin and may be displacing native prosobranch snails here and elsewhere in the West (see Murray, 1970; Williams et al., 1985), although rigorous documentation of this phenomenon and elucidation of its mechanism are lacking.

[2] Note that the widespread Watercress is often segregated as *Nasturtium* (Nelson, 1925).

SYSTEMATICS

Family Hydrobiidae Troschel, 1857

Pyrgulopsis Call & Pilsbry, 1886

Type species: *Pyrgula nevadensis* Stearns, 1883; original designation.

Diagnosis: A North American freshwater genus distinguished from other taxa assigned to the subfamily Nymphophilinae by the combination of small size, relatively thin, and generally ovate to ovate-conic shell, and penis having relatively few glands. Differs from similar *Nymphophilus* Taylor, 1966b (locally endemic in northern Mexico) in several features of the radular teeth (e.g., narrower central teeth, narrower basal tongue on the central teeth, narrower central cusps on the central and lateral teeth), simpler gonadal morphology, longitudinal (not transverse) bursa copulatrix, and superficial (not raised) position of the vas deferens on the neck.

Remarks: Phylogenetic relationships among the new taxa described herein are not known. Thus, for sake of convenience and to aid the reader attempting to identify material, these species instead are treated according to their geographic distributions, which are grouped into major hydrographic units as indicated below. Note that although local endemism is frequent in this fauna, several species occur in more than one of these drainages.

(a) Death Valley system. The hydrobiid fauna of this large drainage, which may or may not have emptied into the Colorado River during the Quaternary (Brown & Rosen, 1995), was recently reviewed by Hershler & Pratt (1990). During the current survey, new material was obtained from a few portions of the drainage in southwestern Nevada.

(b) Colorado River basin. This includes the current Colorado River drainage in southern Nevada as well as several large basins in the eastern half of the state that drained to the Colorado in pluvial times (Hubbs & Miller, 1948).

(c) Isolated basins in Nevada. This includes a large number of valleys whose pluvial waters were not integrated with either Lake Lahontan or Lake Bonneville.

(d) Lahontan Basin. A very large pluvial drainage encompassing the Carson, Humboldt, Susan, Quinn, Truckee, and Walker River basins.

(e) Oregon Lakes. An area of isolated basins in southeast Oregon and northeast California, north of the Lahontan Basin.

(f) Bonneville Basin. A huge drainage, occupying much of western Utah, and portions of southeast Idaho and eastern Nevada, which contained the largest pluvial lake in the Great Basin.

Scanning electron micrographs of shells of each new species are shown in Figures 6–10. Scanning electron micrographs of shell protoconch (Figure 11), operculum (Figures 12, 13), and radula (Figures 14–16) are illustrated for small subsets of the new species in order to show variation in relevant features. Type and nontype shells (Figures 17–25), and distal female genitalia and penis (Figures 26–48) are illustrated for each of the new species following the text, along with maps showing distribution of the species (Figures 49–56).

SYSTEMATICS

Species from the Death Valley System

Pyrgulopsis micrococcus (Pilsbry, 1893)

Amnicola micrococcus Pilsbry in Stearns, 1893:277, fig. 1.
Fontelicella (*Microamnicola*) *micrococcus* (Pilsbry in Stearns, 1893), Gregg & Taylor, 1965:109 [transfer to *Fontelicella* (*Microamnicola*)].
Fontelicella micrococcus (Pilsbry in Stearns, 1893), Taylor, 1975:123 [literature compilation].
Pyrgulopsis micrococcus (Pilsbry in Stearns, 1893), Hershler & Thompson, 1987:28–30 [transfer to *Pyrgulopsis*].-Hershler, 1994:50, 52 [figures, literature compilation].

Diagnosis: Small to medium-sized, with sub-globose to ovate-conic shell. Penis medium-sized, filament medium length, lobe short. Penial ornament a small-medium terminal gland.

Type locality: Small spring in Oasis Valley, Nevada.

Remarks: *Pyrgulopsis micrococcus* is contrasted with *P. **turbatrix*** below. This species is widespread in the eastern portion of the Death Valley system (Hershler & Pratt, 1990:fig. 5). Collections made during the survey are all in the immediate vicinity of the type locality. Note that populations from Frenchman Flat (Cane Spring) and northern end of the Spring Mountains (Cold Creek, Willow Creek) in southern Nevada assigned to this species by Hershler & Pratt (1990) are herein transferred to *P. **turbatrix*** (described below). The distribution of this species is shown in Figure 49.

Material examined: NEVADA. *Nye County*: Spring, adjacent to HWY 95, Oasis Valley, Amargosa River drainage, T. 10 S, R. 47 E, SE ¼ section 32, USNM 874778.—Spring, east of HWY 95, east end of Oleo Road, Oasis Valley, Amargosa River drainage, T. 11 S, R. 47 E, NW ¼ section 10, USNM 874771.—Spring, 2 km northwest of Beatty, Oasis Valley, Amargosa River drainage, T. 12 S, R. 47 E, SW ¼ section 5, USNM 874758.

Species from the Colorado River Drainage

*Pyrgulopsis **fausta*** Hershler, sp. nov.

Corn Creek pyrg

(Figures 6A, 12A, 17A, 26A–C)

Etymology: From *faustus* (Latin), lucky; referring to the good fortune that this locally endemic species persists despite a long and continuing period of extensive development in the vicinity of Las Vegas, Nevada.

Diagnosis: Small, with sub-globose shell. Penis large, filament medium length, lobe short. Penial ornament a small terminal gland, large penial gland, small Dg1, dot-like Dg2, large Dg3, and large ventral gland.

Description: Shell (Figures 6A, 17A) sub-globose, width/height, 83–94%; height 1.4–1.7 mm; width, 1.3–1.5 mm; whorls, 3.25–3.75. Protoconch 1.3 whorls, diameter 0.33 mm, initial 1.0 whorl finely wrinkled (sculpture coarser at apex), later portion near smooth, sculpture occasionally coalescing to form weak spiral elements. Teleoconch whorls moderately convex, usually shouldered. Aperture broadly ovate, adnate or slightly separated from body whorl. Inner lip slightly thickened, without columellar shelf. Outer lip slightly thickened, weakly prosocline, without sinuation. Umbilicus rimate or perforate. Periostracum light tan.

Operculum (Figure 12A) ovate, amber; nucleus slightly eccentric; dorsal surface weakly frilled; outer margin sometimes having weak rim. Attachment scar sometimes slightly thickened between nucleus and inner edge.

Radula 600 × 80 μm, with 75 rows of teeth. Central tooth 21 μm wide, with medium indented dorsal edge; lateral cusps 5–6; central cusp narrow, daggerlike; basal cusps small. Basal tongue narrow V-shaped, basal sockets medium depth. Lateral tooth formula 4(5)-1–5; weakly flexed; outer wing 200% of cutting edge length. Inner marginal teeth with 25–28 cusps; cutting edge occupying 33% of length of tooth. Outer marginal teeth with 34–37 cusps; cutting edge occupying 20% of length of tooth. Stomach slightly longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum very small.

Cephalic tentacles unpigmented or having a few scattered brown granules on dorsal surfaces. Snout, foot unpigmented; opercular lobe unpigmented or having band of grey-black subepithelial pigment along inner edge. Neck having scattered grey, subepithelial pigment. Pallial roof,

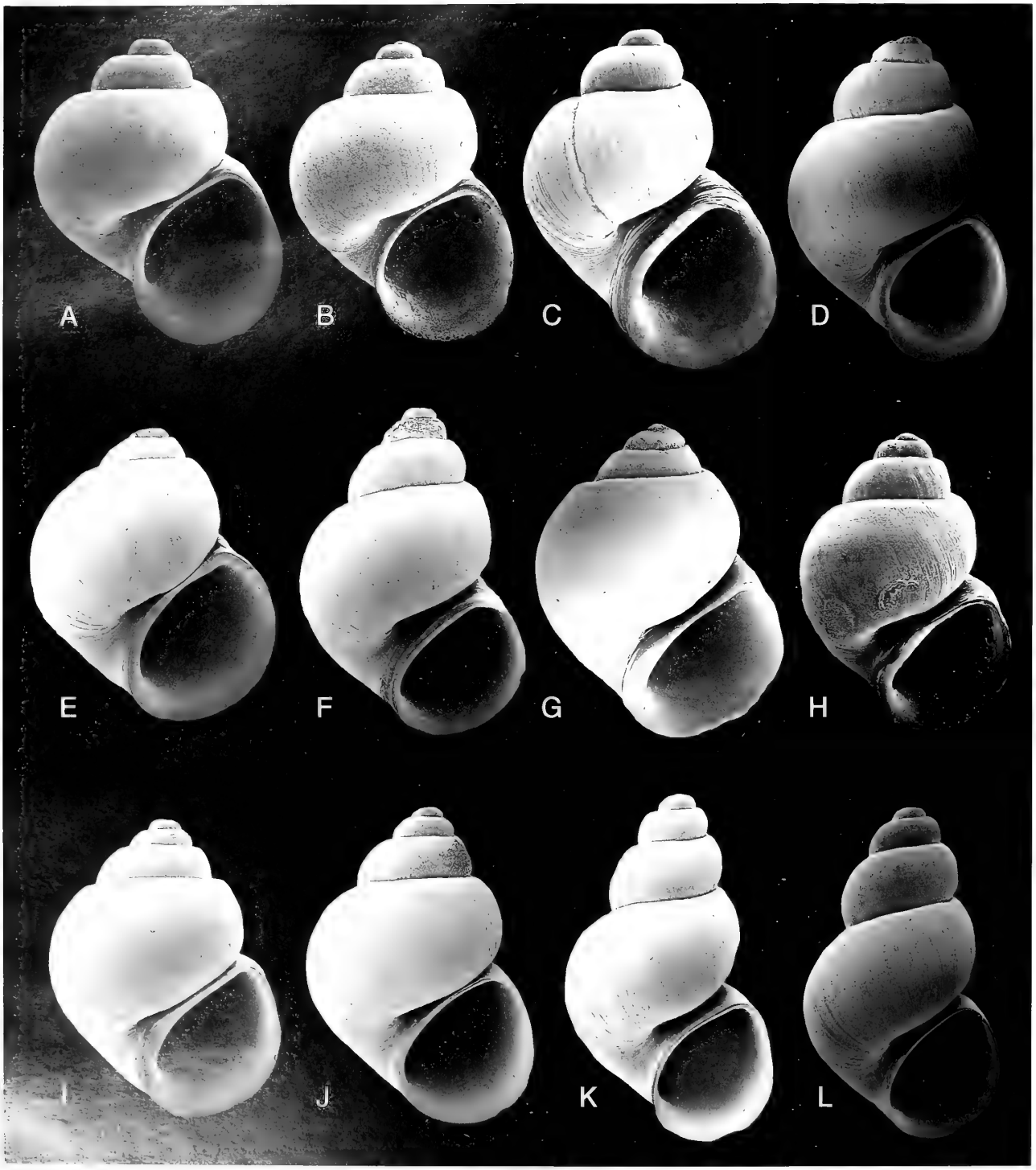


Figure 6

shells of *Pyrgulopsis* species. A. ***P. fausta,*** USNM 860765 (shell height, 1.7 mm). B. ***P. deaconi,*** USNM 860676 (1.9 mm). C. ***P. coloradensis,*** USNM 860677 (1.6 mm). D. ***P. montana,*** USNM 860694 (2.5 mm). E. ***P. hubbsi,*** USNM 860690 (3.1 mm). F. ***P. sathos,*** USNM 860691 (3.0 mm). G. ***P. breviloba,*** USNM 860689 (1.8 mm). H. ***P. lata,*** USNM 860697 (1.9 mm). I. ***P. gracilis,*** USNM 860698 (1.8 mm). J. ***P. marcida,*** USNM 860711 (3.0 mm). K. *P. turbatrix*, USNM 860699 (3.0 mm). L. ***P. sterilis,*** USNM 860714 (3.6 mm).

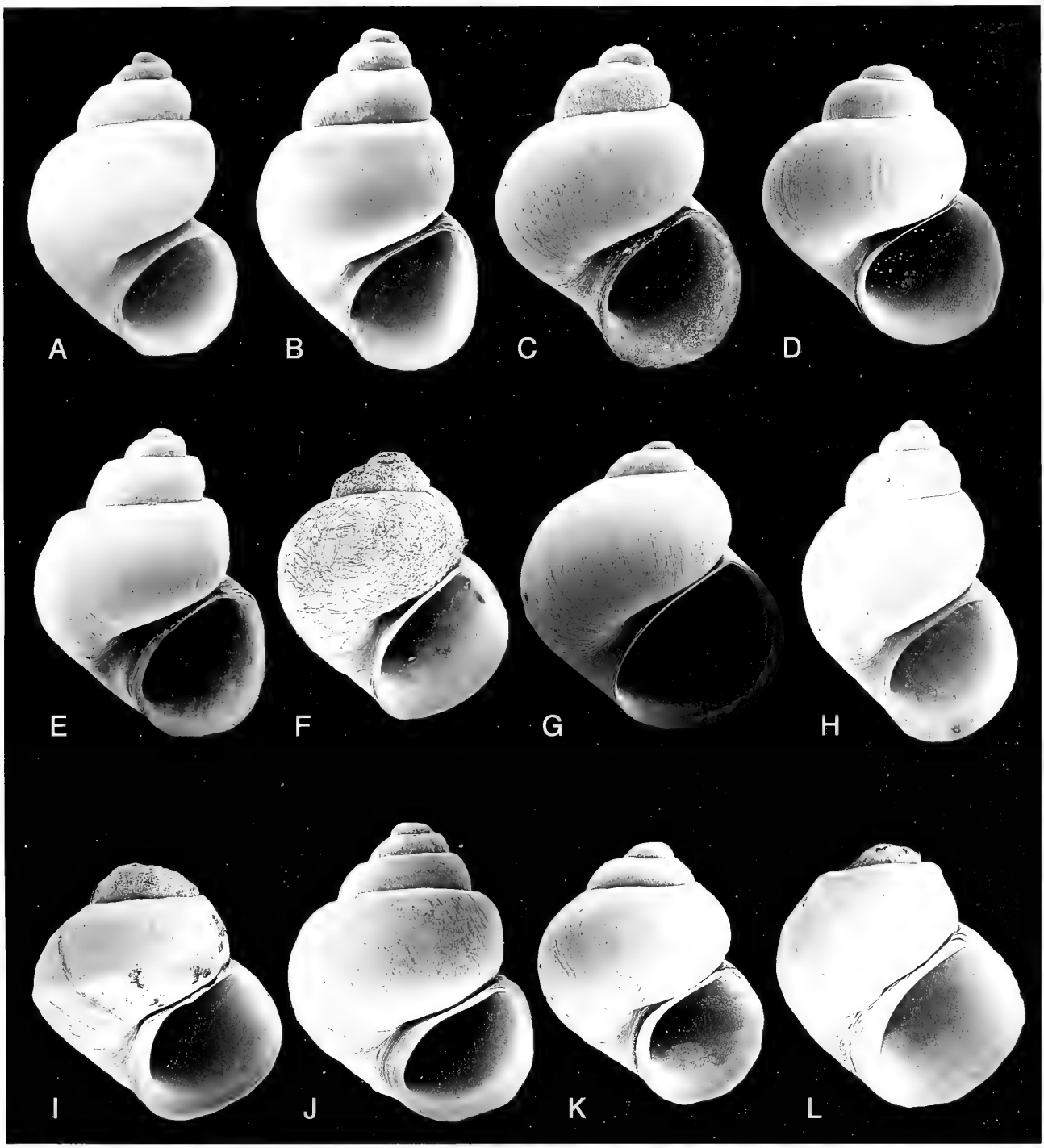


Figure 7

Shells of *Pyrgulopsis* species. A. ***P. ruinosa,*** USNM 860700 (2.8 mm). B. ***P. sublata,*** USNM 860724 (2.4 mm). C. ***P. lockensis,*** USNM 860679 (1.9 mm). D. ***P. papillata,*** USNM 860678 (1.9 mm). E. ***P. carinata,*** USNM 860680 (2.1 mm). F. ***P. aloba,*** USNM 860681 (1.2 mm). G. ***P. villacampae,*** USNM 860712 (2.4 mm). H. ***P. anatina,*** USNM 860710 (2.3 mm). I. ***P. planulata,*** USNM 860686 (1.3 mm). J. ***P. sulcata,*** USNM 860683 (1.4 mm). K. ***P. orbiculata,*** USNM 860682 (2.1 mm). L. ***P. neritella,*** USNM 860684 (1.3 mm).

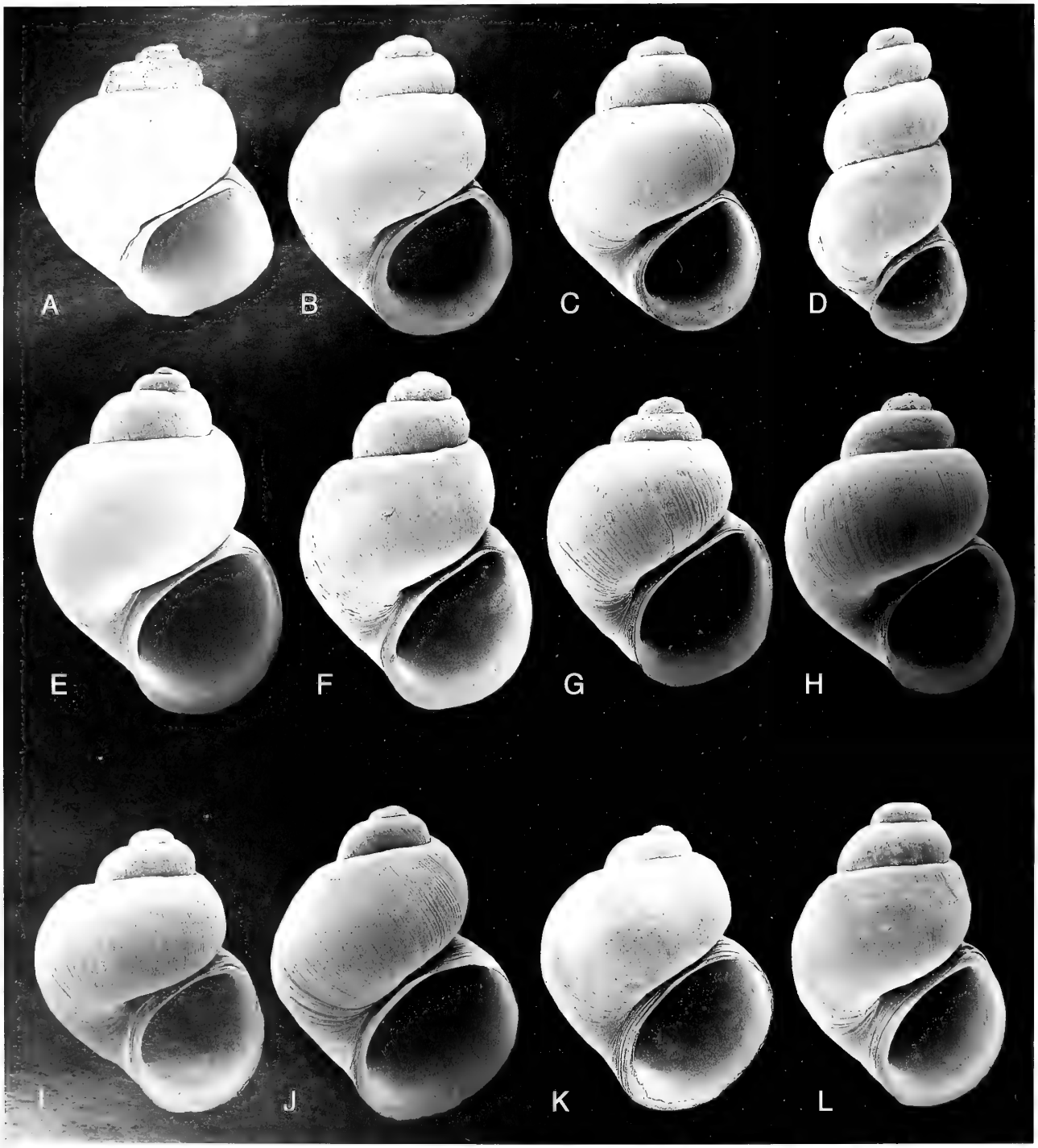


Figure 8

Shells of *Pyrgulopsis* species. A. *P.* ***landyei,*** USNM 860685 (1.3 mm). B. *P.* ***serrata,*** USNM 860719 (3.2 mm). C. *P.* ***cruciglans,*** USNM 860719 (3.3 mm). D. *P.* ***dixensis,*** USNM 860688 (1.6 mm). E. *P.* ***aurata,*** USNM 860696 (3.2 mm). F. *P.* ***longiglans,*** USNM 860701 (3.4 mm). G. *P.* ***militaris,*** USNM 860704 (2.4 mm). H. *P.* ***umbilicata,*** USNM 860705 (3.2 mm). I. *P.* ***limaria,*** USNM 860706 (2.6 mm). J. *P.* ***notidicola,*** USNM 860707 (3.0 mm). K. [illegible] USNM 860708 (2.6 mm). L. *P.* ***imperialis,*** USNM 860716 (2.3 mm).

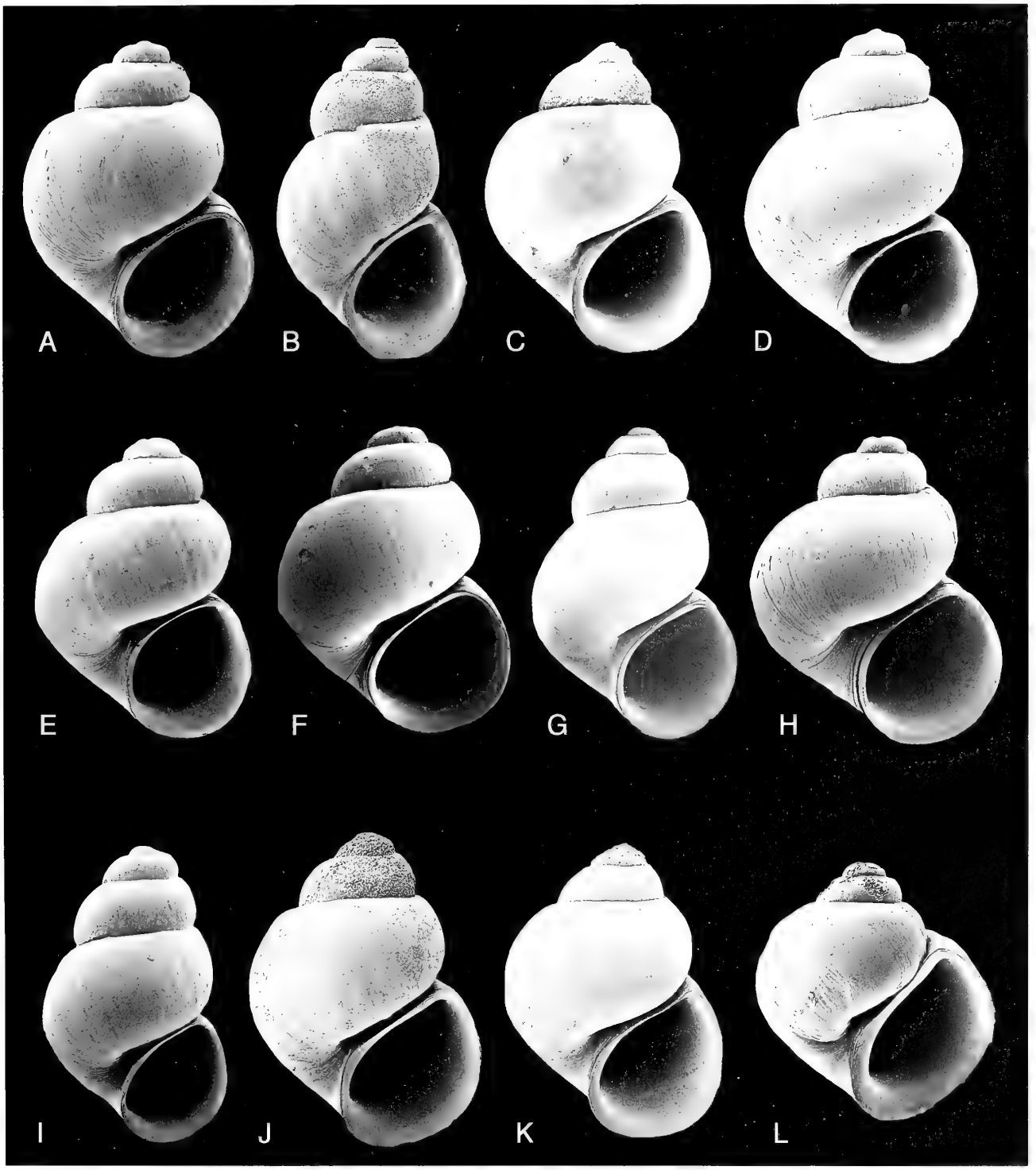


Figure 9

Shells of *Pyrgulopsis* species. A. ***P. sadai,*** USNM 860702 (3.8 mm). B. ***P. augustae,*** USNM 860687 (3.3 mm). C. ***P. pictilis,*** USNM 860713 (2.6 mm). D. ***P. basiglans,*** USNM 860692 (2.8 mm). E. ***P. bifurcata,*** USNM 860693 (2.3 mm). F. ***P. pellita,*** USNM 860715 (2.5 mm). G. ***P. leporina,*** USNM 860717 (3.6 mm). H. ***P. humboldtensis,*** USNM 860718 (2.2 mm). I. ***P. hamlinensis,*** USNM 860695 (1.9 mm). J. ***P. peculiaris,*** USNM 860703 (2.0 mm). K. ***P. anguina,*** USNM 860725 (2.5 mm). L. ***P. saxatilis,*** USNM 860726 (1.2 mm).

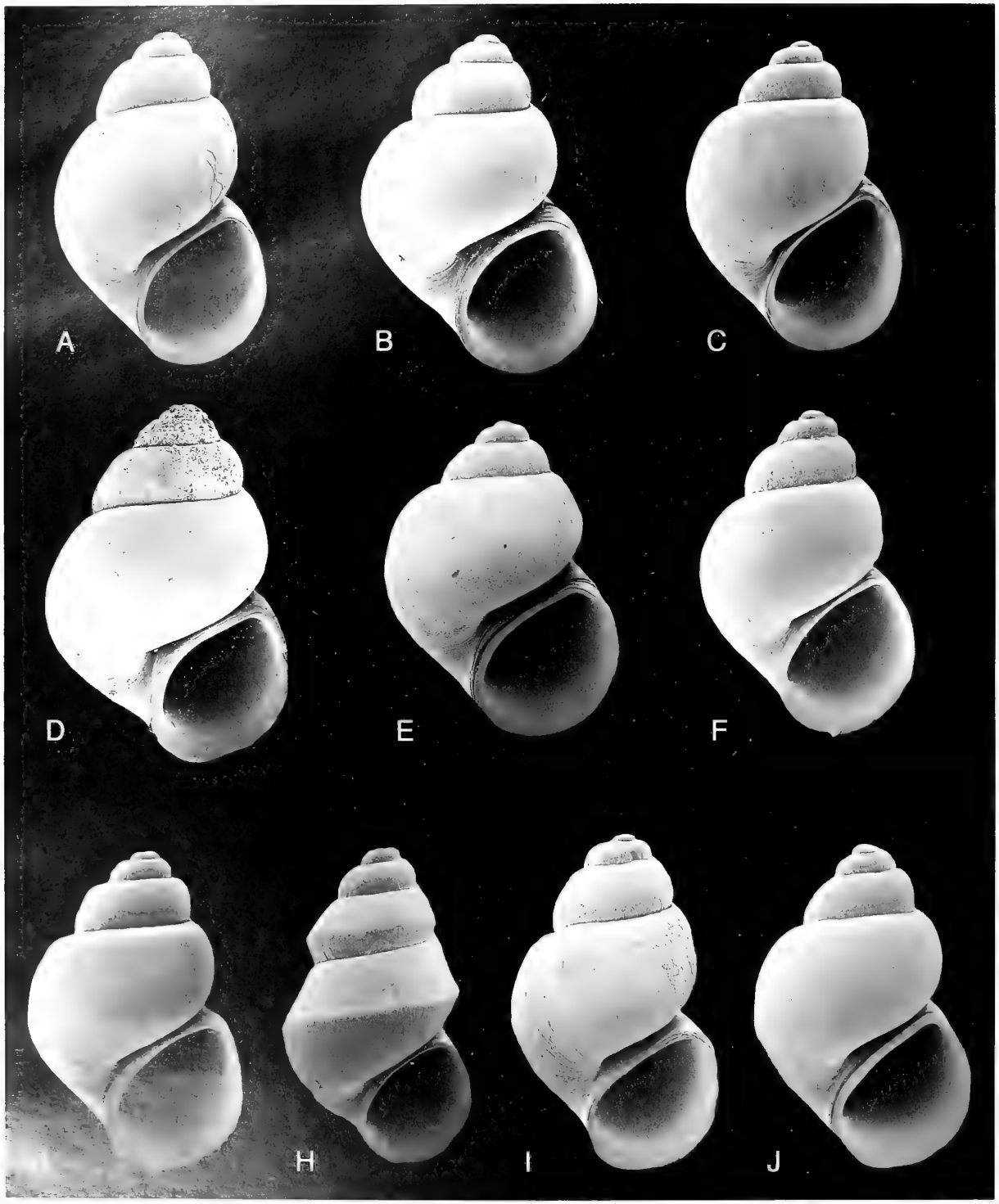


Figure 10

Shells of *Pyrgulopsis* species. A. *P.* ***variegata,*** USNM 860723 (2.3 mm). B. *P.* ***hovinghi,*** USNM 860720 (2.6 mm). C. *P.* ***millenaria,*** USNM 860721 (2.4 mm). D. *P.* ***lentiglans,*** USNM 860722 (1.7 mm). E. *P.* ***plicata,*** USNM 860727 (2.2 mm). F. *P.* ***fusca,*** USNM 860728 (2.7 mm). G. *P.* ***chamberlini,*** USNM 860729 (2.3 mm). H. *P.* ***inopinata,*** USNM 860730 (2.7 mm). I. *P.* ***nonaria,*** USNM 860731 (2.6 mm). J. *P.* ***transversa,*** USNM 860732 (2.3

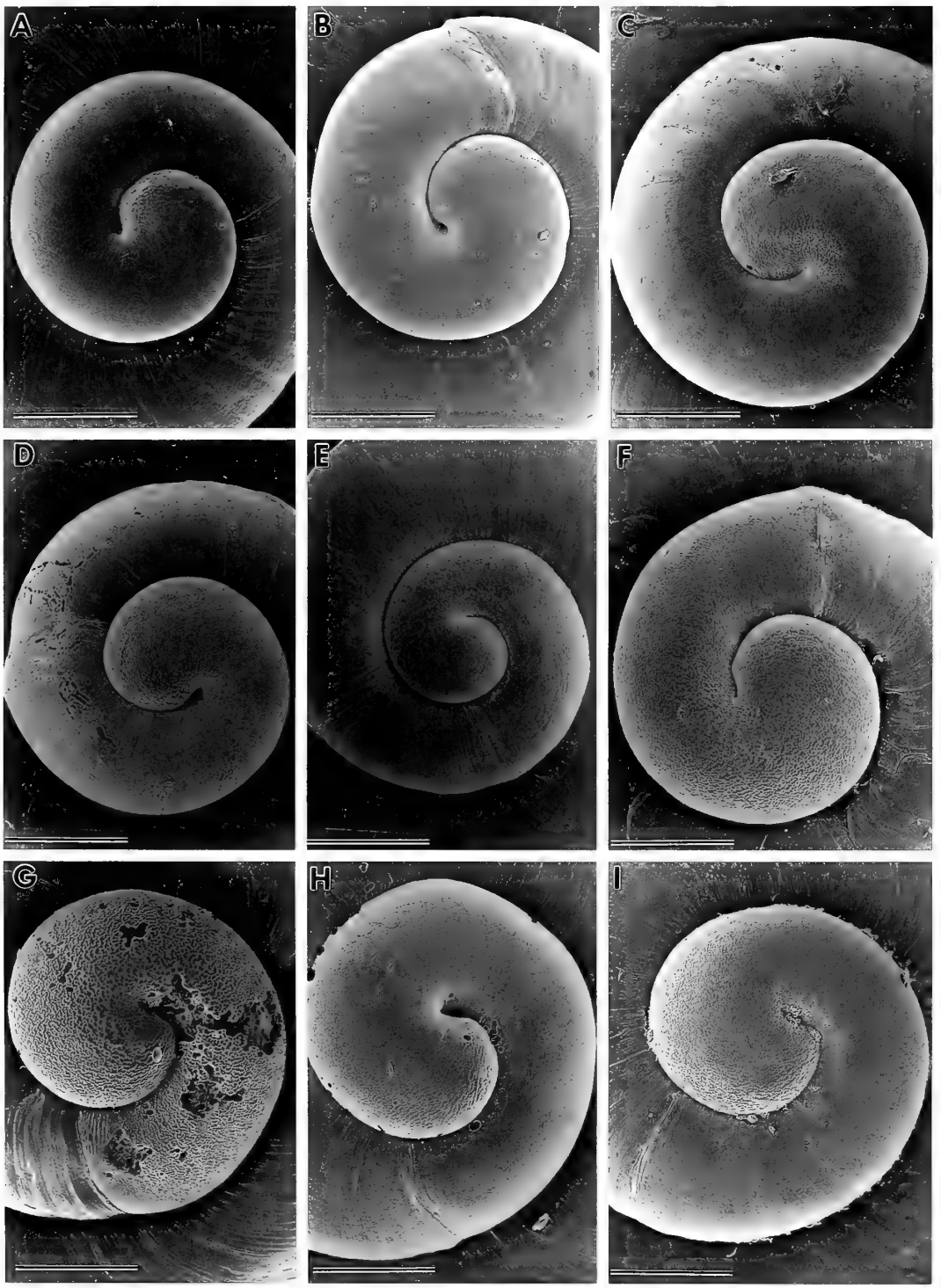
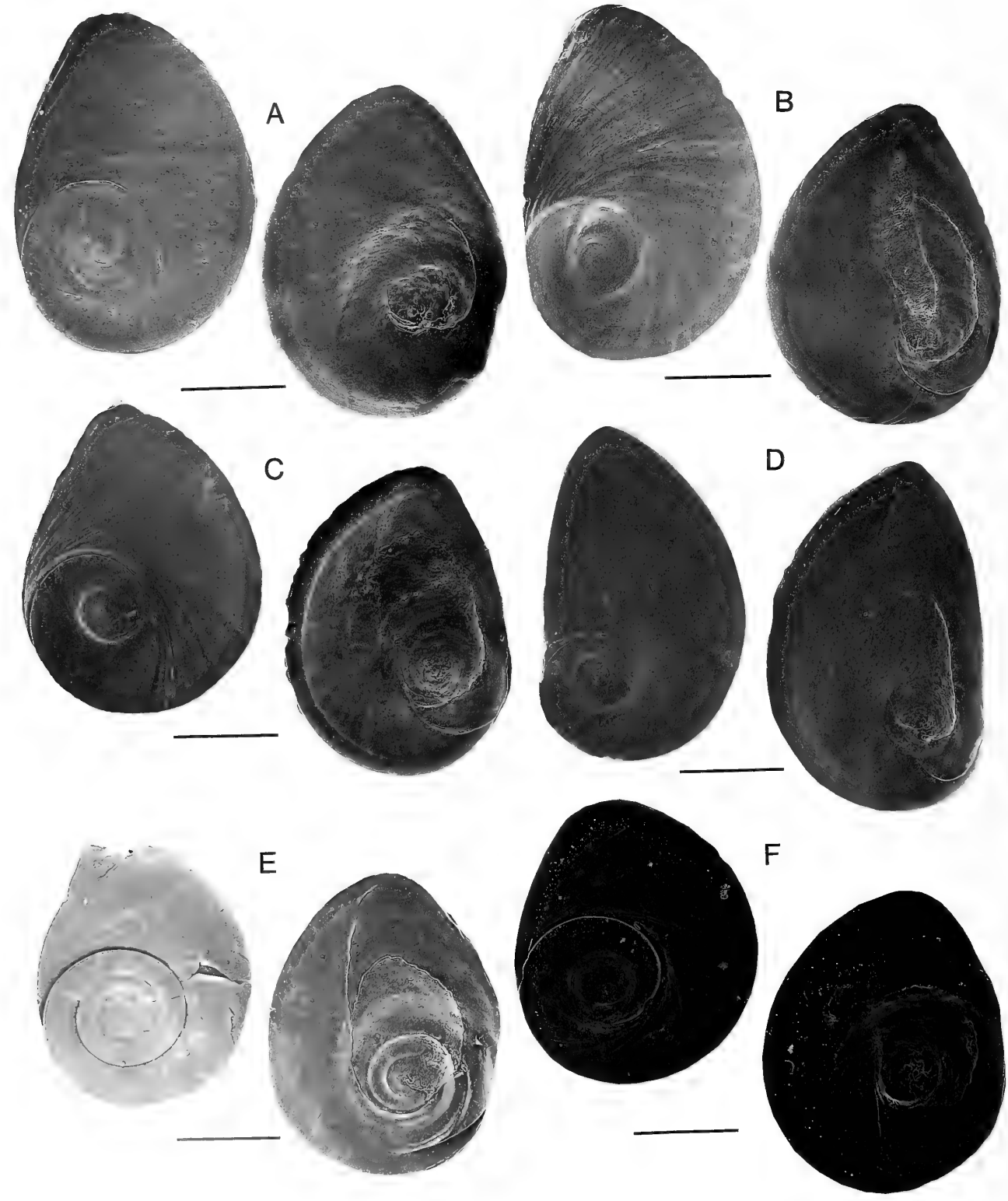


Figure 11

Shell protoconchs of *Pyrgulopsis* species. A. ***P. deaconi,*** USNM 860676 (bar = 0.12 mm). B. ***P. montana,*** USNM 860694 (bar = 0.15 mm). C. ***P. breviloba,*** USNM 860689 (bar = 0.11 mm). D. ***P. gracilis,*** USNM 860698 (bar = 0.13 mm). E. ***P. papillata,*** USNM 860678 (bar = 0.16 mm). F. ***P. sulcata,*** USNM 860683 (bar = 0.10 mm). G. ***P. neritella,*** USNM 860684 (bar = 0.10 mm). H. ***P. saxatilis,*** USNM 860726 (bar = 0.10 mm). I. ***P. hovinghi,*** USNM 860720 (bar = 0.11 mm).


A
B
C
D
E
F

visceral coil medium to uniform black. Ventral surface of penial filament pigmented with scattered black granules.

Ctenidial filaments 11, without pleats; ctenidium slightly overlapping pericardium posteriorly. Osphradium small, ovate, centered slightly anterior to middle of ctenidium. Renal gland longitudinal; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.75 whorl, filling 50% of digestive gland behind stomach, abutting posterior edge of stomach anteriorly. Distal female genitalia shown in Figure 26A. Albumen gland having short or no pallial component. Capsule gland shorter, narrower than albumen gland, sub-circular in section; rectal furrow weak or absent. Ventral channel broadly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a single, tight circular loop. Oviduct and bursal duct joining well behind pallial wall; common duct broad, sometimes embedded in albumen gland distally. Bursa copulatrix as wide and almost as long as albumen gland, broadly ovate-pyriform, longitudinal, posterior to and pressed against edge of albumen gland. Bursal duct originating from anterior edge slightly dorsal to midline, long, narrow, but broadening distally, lying in shallow depression in albumen gland. Seminal receptacle small, narrow, overlapping anterior bursa along ventral edge, largely posterior to albumen gland.

Testis 0.75–1.0 whorl, filling more than 50% of digestive gland behind stomach, abutting posterior edge of stomach. Prostate gland large, bean-shaped, entirely visceral, narrowly ovate in section. Proximal pallial vas deferens having twist or sharp bend. Penis (Figure 26B, C) large; base nearly square, smooth; filament slightly shorter than base, broad, tapering, longitudinal; lobe shorter than filament, knoblike, longitudinal. Terminal gland short, narrow, slightly curved, sometimes divided into two units, transverse, extending onto both dorsal and ventral surfaces. Penial gland filling entire length and width of filament, slightly overlapping penis base. Dg1 short, transverse, positioned near outer edge proximal to penial gland. Dg2 dotlike, near inner edge. Dg3 long, curved, borne on low swelling. Dorsal glands sometimes accompanied by small glandular dot between Dg1 and Dg2. Ventral gland large, narrow, sometimes divided into two units, borne on low swelling, curving from near outer edge at mid-length to distal inner edge and extending to edge of lobe. Penial duct almost straight, near outer edge.

Type locality: Corn Creek Springs, Las Vegas Valley, Clark Country, Nevada, T. 17 S, R. 59 E, NE ¼ section 34. Corn Creek Springs lie within the Desert National Wildlife Refuge Complex (Figure 49) and comprise a main spring, now modified by a cement-lined outflow, and several smaller springs and seeps, all of which are thermal (ca. 23°C.) The type locality is a small spring several hundred meters south of the main spring. Holotype, USNM 874757 (Figure 17A), collected by D. W. Sada, 6 June 1992; paratypes, USNM 860765.

Remarks: Among the group of *Pyrgulopsis* having a full complement of glands on the penis, this species is distinguished by a very large penial gland (covering all of the filament) and a uniquely elongate ventral gland that crosses the entire width of the penis and extends along the inner edge of the penis distally. These features are approached in *P. **deaconi*** (described below), which occurs in the nearby Spring Mountains, although the terminal and ventral glands in *P. **deaconi*** are not as large, and the ventral gland does not extend to the inner edge as in *P. **fausta.*** *Pyrgulopsis **fausta*** is further distinguished from this species by its squatter penis with broader filament, larger penial gland, and presence of Dg1 and Dg2.

Material examined: NEVADA. *Clark County:* Corn Creek Springs (main spring), USNM 873183, USNM 873397, USNM 873413, USNM 873419.—Corn Creek Springs (small seep east of above), USNM 873175.—Corn Creek Springs (small spring south of main spring), USNM 860765, USNM 874757.—Corn Creek Springs, USNM 873453.

*Pyrgulopsis **deaconi*** Hershler, sp. nov.

Spring Mountains pyrg

(Figures 6B, 11A, 17B, C, 26D–G)

Etymology: Named after James Deacon (University of Nevada, Las Vegas), in recognition of his numerous studies of the spring biota of southern Nevada over the past 35 years.

Diagnosis: Small, with sub-globose shell. Penis large; filament medium length, lobe short. Penial ornament a small terminal gland, large penial gland, large Dg3, and large ventral gland.

Description: Shell (Figures 6B, 17B, C) sub-globose, width/height, 79–89%; height, 1.5–1.9 mm; width, 1.3–1.7 mm; whorls, 3.5–3.75. Protoconch (Figure 11A) 1.25 whorls, diameter 0.26 mm, initial 0.75 whorl finely wrinkled (sculpture coarser near apex), later portion nearly

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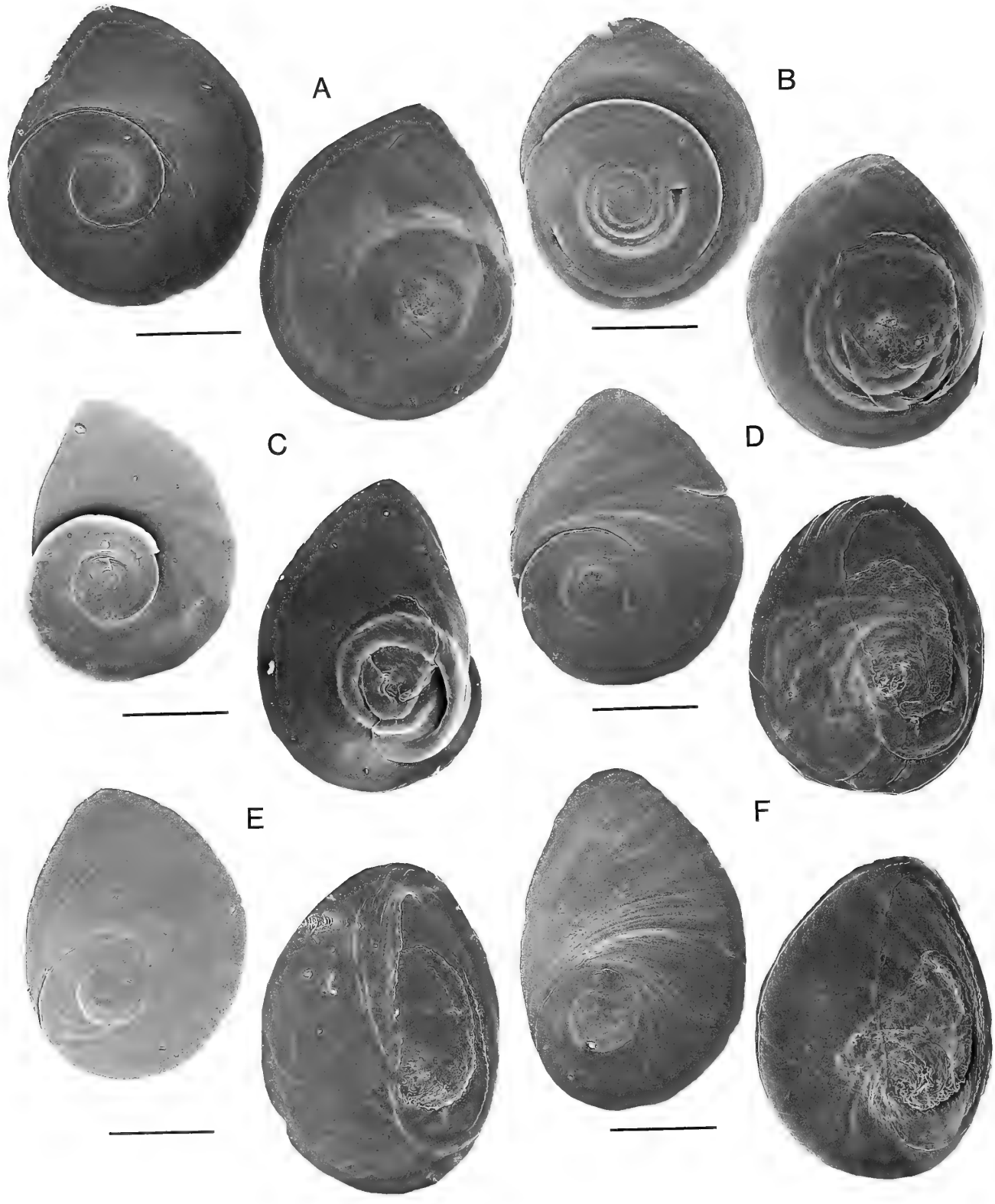
Figure 12

Opercula of *Pyrgulopsis* species. A. *P. **fausta,*** USNM 860765 (bar = 0.26 mm). B. *P. **montana,*** USNM 860694 (bar = 0.26 mm). C. *P. **sathos,*** USNM 860691 (bar = 0.76 mm). D. *P. **lata,*** USNM 860697 (bar = 0.22 mm). E. *P. **sublata,*** USNM 860724 (bar = 0.31 mm). F. *P. **lockensis,*** USNM 874879 (bar = 0.28 mm).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smooth. Teleoconch whorls moderately convex, usually shouldered. Aperture broadly ovate, narrowly adnate above or slightly separated from body whorl. Inner lip slightly thickened, without columellar shelf. Outer lip usually thin, prosocline, weakly sinuate. Umbilicus rimate or perforate. Periostracum light tan.

Operculum ovate, amber; nucleus slightly eccentric; dorsal surface weakly frilled; outer margin sometimes having weak rim. Attachment scar thick all around.

Radula 560 × 80 μm, with 62 rows of teeth. Central tooth 25 μm wide, with medium indented dorsal edge; lateral cusps, 4–6; central cusp narrow, daggerlike; basal cusps small. Basal tongue narrow V-shaped, basal sockets medium depth. Lateral tooth formula 3-1-(3–4); weakly flexed; outer wing 150–200% of cutting edge length. Inner marginal teeth with 21–22 cusps; cutting edge occupying 40% of length of tooth. Outer marginal teeth with 30–33 cusps; cutting edge occupying 16% of length of tooth. Stomach slightly longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum very small.

Cephalic tentacles unpigmented or light grey. Snout unpigmented to medium brown-grey. Foot unpigmented to medium grey. Opercular lobe having black subepithelial pigment along inner edge. Neck light grey. Pallial roof, visceral coil black. Ventral surface of penial filament having light to medium cover of black granules, pigment sometimes also present on dorsal surface alongside penial gland.

Ctenidial filaments, 14–15, without pleats; ctenidium overlapping pericardium posteriorly. Osphradium small, ovate, centrally positioned. Renal gland oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 1.0 whorl, filling more than 50% of digestive gland behind stomach, slightly overlapping posterior stomach chamber anteriorly. Distal female genitalia shown in Figure 26D. Albumen gland having medium pallial component. Capsule gland shorter, narrower than albumen gland, sub-circular in section; rectal furrow absent. Ventral channel broadly overlapping capsule gland, distal end slightly separated from gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a single, tight circular loop. Oviduct and bursal duct joining well behind pallial wall; common duct broad, sometimes embedded in albumen gland distally. Bursa copulatrix as wide as albumen gland, medium width, broadly ovate to sub-circular, longitudinal, posterior to and pressed against edge of albumen gland. Bursal duct originating from anterior edge slightly dorsal to mid-line, long, narrow, broadening distally, lying in shallow depression in albumen gland. Seminal receptacle small, ovate-narrow, overlapping anterior bursa along ventral edge posterior to albumen gland.

Testis 1.0 whorl, filling more than 50% of length of digestive gland behind stomach; overlapping posterior stomach chamber anteriorly. Prostate gland ovate, pallial portion short, narrowly ovate in section. Proximal pallial vas deferens thick, reflexed. Penis (Figure 26E–G) large, base rectangular, sometimes weakly folded along inner edge; filament much shorter than base, medium width, tapering; lobe short, knoblike, oblique. Terminal gland short, narrow to sub-circular, sometimes slightly curved, transverse-oblique, largely on ventral surface. Penial gland filling most of filament length and width, slightly overlapping penis base. Dg3 long, borne on low swelling, sometimes flanked by small glandular dot proximally. Ventral gland large, narrow, often divided into two units, borne on low swelling, positioned between outer edge and mid-line. Penial duct near straight, near outer edge.

Type locality: Red Spring, Red Rock Canyon Recreation Lands, Las Vegas Valley, Clark County, Nevada, T. 21 S, R. 59 E, SW ¼ section 6. Holotype, USNM 874454 (Figure 17B), collected by J. J. Landye, 2 January, 1992; paratypes, USNM 860676. The type locality is a small rheocrene that has been moderately impacted by recreational activities.

Remarks: *Pyrgulopsis* ***deaconi*** is contrasted with *P.* ***fausta*** above. This species is restricted to the Spring Mountains, in drainages of Las Vegas and Pahrump Valleys (Figure 49). The population at Manse Ranch on the floor of Pahrump Valley now is extinct as the spring dried in 1975 (Soltz & Naiman, 1978:24), presumably as a result of local groundwater withdrawal (Minckley & Deacon, 1968:1429).

Material examined: NEVADA. *Clark County:* Red Spring, USNM 860676, USNM 873355, USNM 874084, USNM 874108, USNM 874454, USNM 874457.—Willow Spring, Las Vegas Valley, T. 20 S, R. 58 E, SW ¼ section 33, USNM 873452, USNM 874085, USNM 874456.—Kiup Spring, Pahrump Valley, T. 20 S, R. 56 E, SE ¼ section 31, USNM 854737, USNM 873351, USNM 874390.—*Nye County:* Spring, Manse Ranch, Pahrump Valley, T. 21 S, R. 54 E, NW ¼ section 3, SBMNH uncat.

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Figure 13

Opercula of *Pyrgulopsis* species. A. ***P. villacampae,*** USNM 860712 (bar = 0.44 mm). B. ***P. planulata,*** USNM 860686 (bar = 0.17 mm). C. ***P. dixensis,*** USNM 860688 (bar = 0.15 mm). D. ***P. basiglans,*** USNM 860692 (bar = 0.22 mm). E. ***P. humboldtensis,*** USNM 860718 (bar = 0.31 mm). F. ***P. plicata,*** USNM 860727 (bar = 0.28 mm).

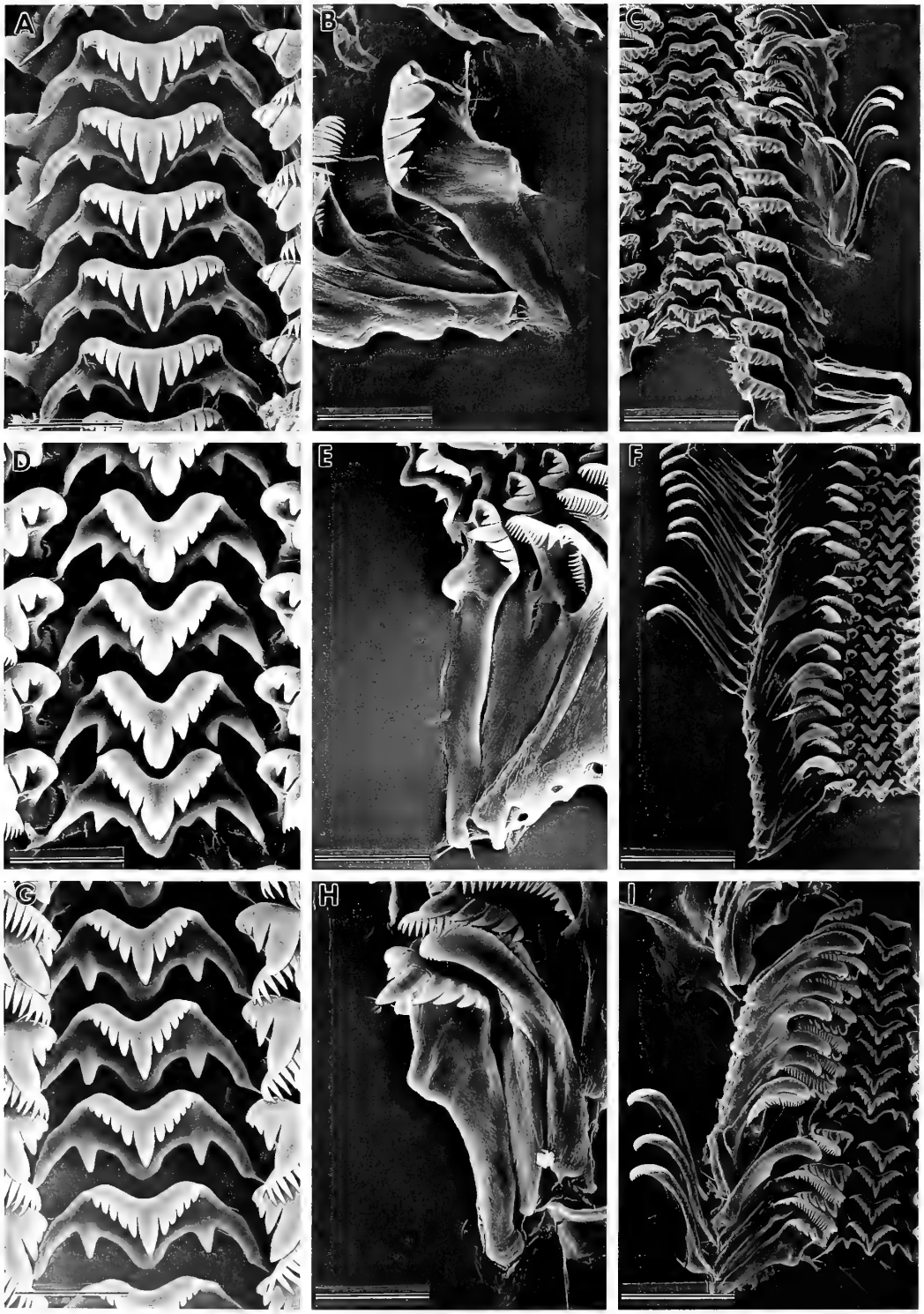


Figure 14

Radulae of *Pyrgulopsis* species. A–C. ***P. hubbsi,*** USNM 874776 (bars = 22 μm, 24 μm, 67 μm, respectively). D–F. ***P. breviloba,*** USNM 860689 (bars = 11 μm, 17 μm, 46 μm, respectively). G–I. ***P. lockensis,*** USNM 874879 (bars = 14 μm, 14 μm, 35 μm, respectively). Photographs show (from left to right) central teeth, lateral teeth, and general view of portion of radula ribbon.

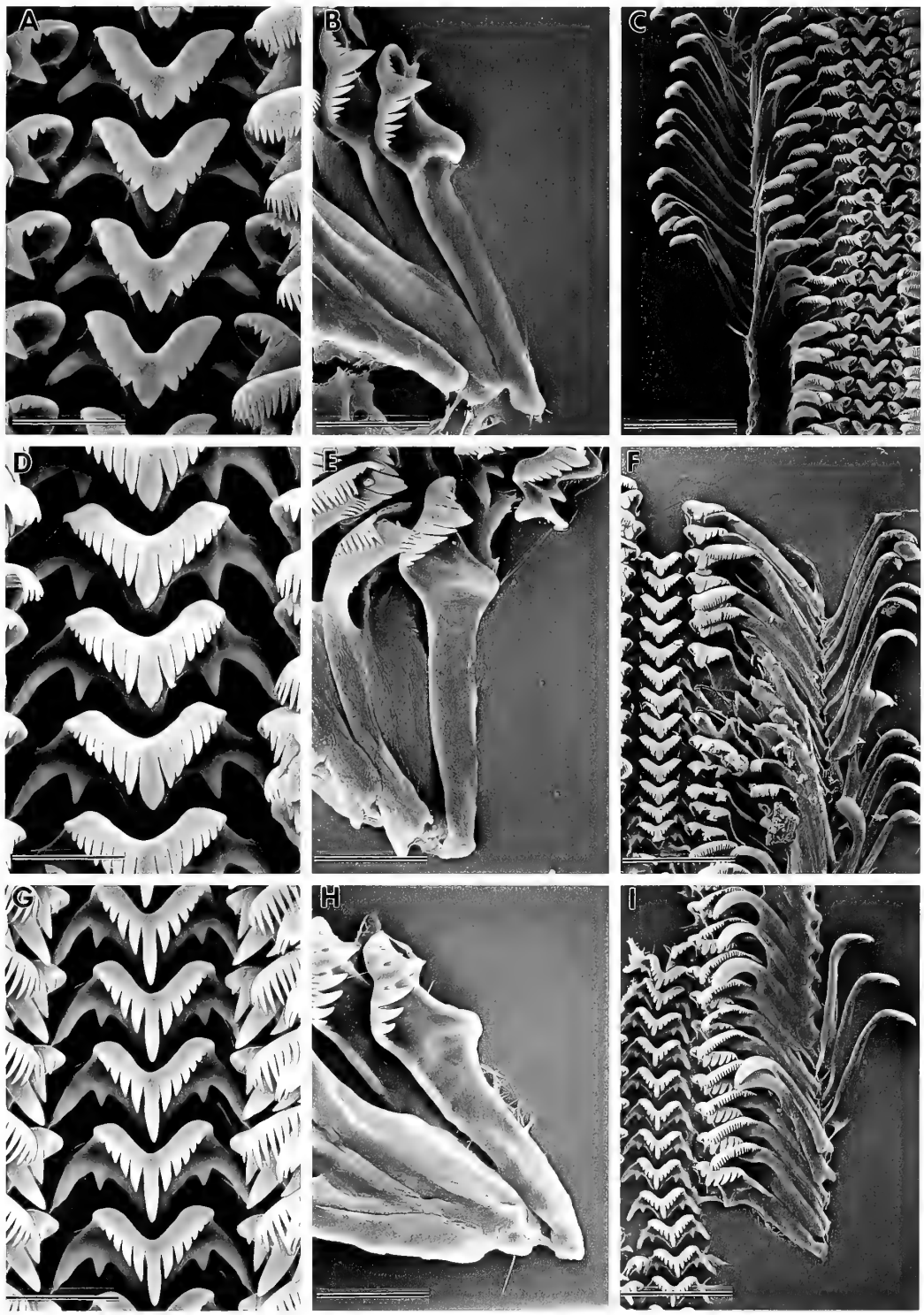


Figure 15

Radulae of *Pyrgulopsis* species. A–C. ***P. planulata,*** USNM 860686 (bars = 8 μm, 12 μm, 43 μm, respectively). D–F. ***P. serrata,*** USNM 860719 (bars = 8 μm, 13 μm, 38 μm, respectively). G–I. ***P. militaris,*** USNM 860704 (bars = 10 μm, 13 μm, 33 μm, respectively). Photographs show (from left to right) central teeth, lateral teeth, and general view of portion of radula ribbon.

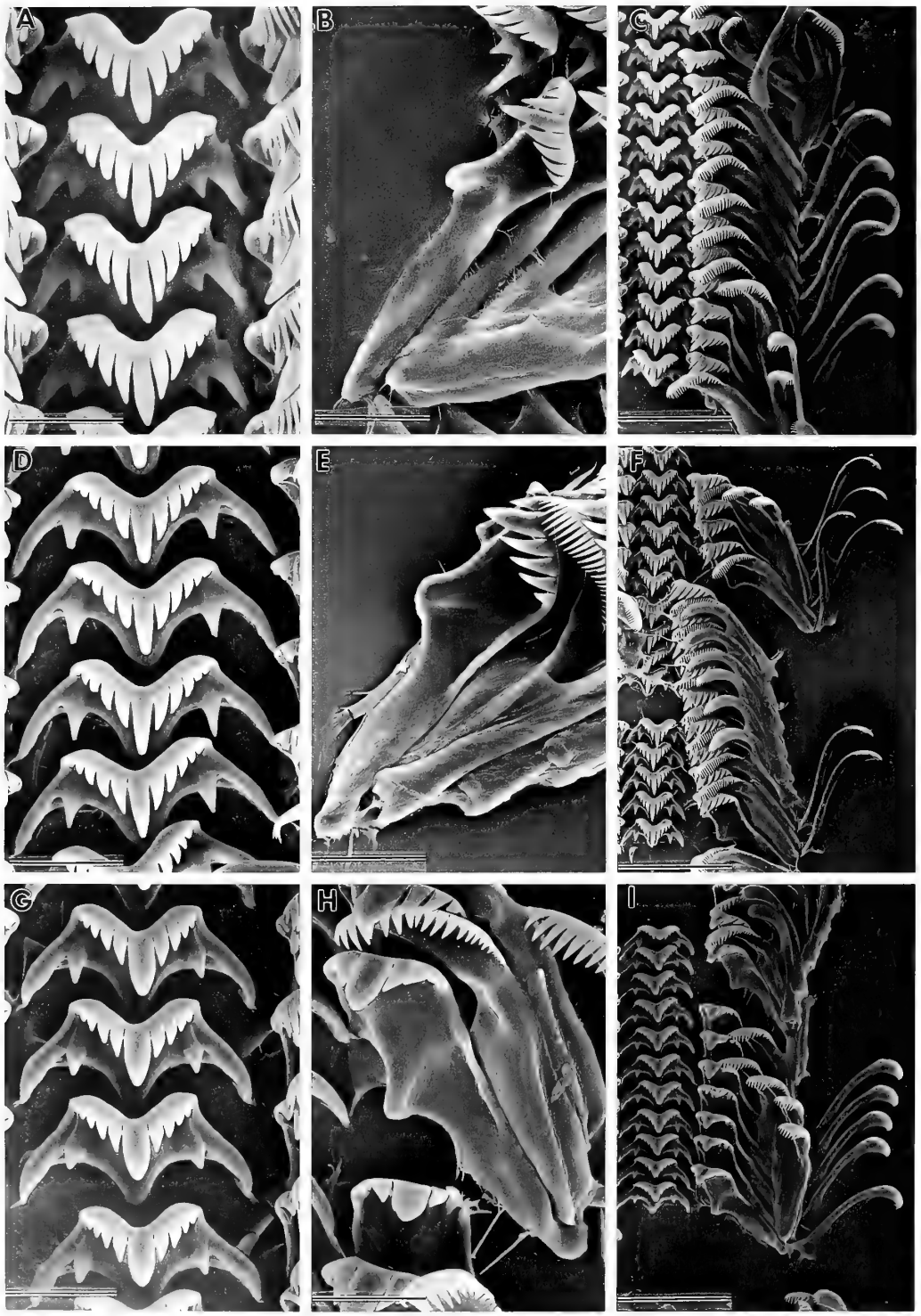


Figure 16

Radulae of *Pyrgulopsis* species. A–C. ***P. saxatilis,*** USNM 860726 (bars = 8 μm, 10 μm, 24 μm, respectively). D–F. *P. **hovinghi,*** USNM 874715 (bars = 11 μm, 15 μm, 46 μm, respectively). G–I. ***P. transversa,*** USNM 860732 (bars = 13 μm, 14 μm, 41 μm, respectively). Photographs show (from left to right) central teeth, lateral teeth, and general view of portion of radula ribbon.

Pyrgulopsis **coloradensis** Hershler, sp. nov.

Blue Point pyrg

(Figures 6C, 17D, 27A, B)

Etymology: The species name refers to the occurrence of this snail in Colorado River drainage.

Diagnosis: Small, with low trochoid to ovate-conic shell. Penis medium-sized, bladelike, lobe absent. Penial ornament absent.

Description: Shell (Figures 6C, 17D) sub-globose to ovate-conic, width/height, 80–93%; height, 1.2–1.6 mm; width, 1.0–1.3 mm; whorls, 2.75–3.5. Protoconch 1.25 whorls, diameter 0.29 mm, initial 0.75 whorl having well-developed wrinkles, sculpture weakening, becoming near smooth on later portion. Teleoconch whorls medium to highly convex, shouldered. Aperture ovate, usually well separated from body whorl. Inner lip often thick, without columellar shelf. Outer lip slightly thickened, orthocline, without sinuation. Umbilicus perforate, umbilical region sometimes excavated and having weak adaxial ridge. Periostracum light tan.

Operculum ovate, amber, nuclear region reddish; nucleus slightly eccentric; dorsal surface weakly frilled. Attachment scar slightly thickened all around.

Radula 460 × 64 μm, with 66 rows of teeth. Central tooth 16 μm wide, broad, with medium indented dorsal edge; lateral cusps 5–7; central cusp narrow, distally rounded; basal cusps small. Basal tongue broad V-shaped, sockets medium. Lateral tooth formula 4-1-4(5); neck weakly flexed; outer wing 225% of cutting edge length. Inner marginal teeth with 21–25 cusps; cutting edge occupying 30% of length of tooth. Outer marginal teeth with 23–28 cusps; cutting edge occupying 27% of length of tooth. Stomach slightly longer than style sac; stomach chambers equal in size; stomach caecum very small.

Cephalic tentacles medium to dark brown or black. Snout dark brown or black. Sides of foot dark grey or brown; opercular lobe dark along inner edge, sometimes pigmented all around. Neck medium to dark brown or black. Pallial roof, visceral coil uniformly black. Dorsal surface of penial filament having few, scattered black granules distally.

Ctenidial filaments 14, without pleats; ctenidium overlapping pericardium posteriorly. Osphradium medium-sized, narrowly ovate, positioned alongside posterior half of ctenidium. Renal gland horizontal; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.75 whorl, filling more than 50% of digestive gland behind stomach, overlapping posterior and sometimes portion of anterior stomach chambers. Distal female genitalia shown in Figure 27A. Albumen gland without pallial component. Capsule gland slightly longer, but narrower than albumen gland, broadly ovate in section; rectal furrow absent. Ventral channel slightly overlapping capsule gland; longitudinal fold weakly developed. Genital aperture a terminal slit without anterior extension. Coiled oviduct a tight circular loop sometimes preceded by slight twist. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copulatrix short, narrow, clublike, longitudinal, 50% of length posterior to albumen gland. Bursal duct originating from anterior edge, as long as, slightly narrower than bursa. Seminal receptacle medium-sized, narrow, often folded, partly overlapping ventral edge of bursa, extending almost to edge of albumen gland.

Testis 1.5 whorls, filling more than 50% of digestive gland behind stomach, overlapping both stomach chambers and extending to edge of prostate gland. Prostate gland fat bean-shaped, pallial portion large (slightly less than 50%), ovate in section. Proximal pallial vas deferens reflexed. Penis (Figure 27B) medium-sized; gently tapering, base and filament poorly differentiated; inner edge weakly folded or smooth; lobe and glands absent. Penial duct near straight, near outer edge.

Type locality: Blue Point Spring, Colorado River drainage, Clark County, Nevada, T. 18 S, R. 68 E, SW ¼ section 6 (Figure 49). Holotype, USNM 854621 (Figure 17D), collected by R. Hershler, 10 October 1993; paratypes USNM 860677. *Pyrgulopsis* ***coloradensis*** occurs in limited abundance (having become increasingly scarce in the past decade) in this small, thermal (30°C.) rheocrene, which is situated within the Lake Mead National Recreation Area.

Remarks: This isolated local endemic differs from the group of simple-pened species in Railroad Valley by its more elongate shell; simply tapering, smooth penis; and small, narrow bursa copulatrix.

Material examined: NEVADA. *Clark County:* Blue Point Spring, USNM 854621, USNM 854641, USNM 860677, USNM 873347, USNM 873360.

Pyrgulopsis avernalis (Pilsbry, 1935)

Fluminicola avernalis Pilsbry, 1935:92, fig. 1.—Williams et al., 1985:48 [habitat notes].

"*Fluminicola*" *avernalis* (Pilsbry, 1935), Taylor, 1975:40 [literature compilation].—Pratt, 1977:7 [habitat notes].—Taylor, 1983:294 [Miocene Muddy Creek Formation, Clark County, Nevada].

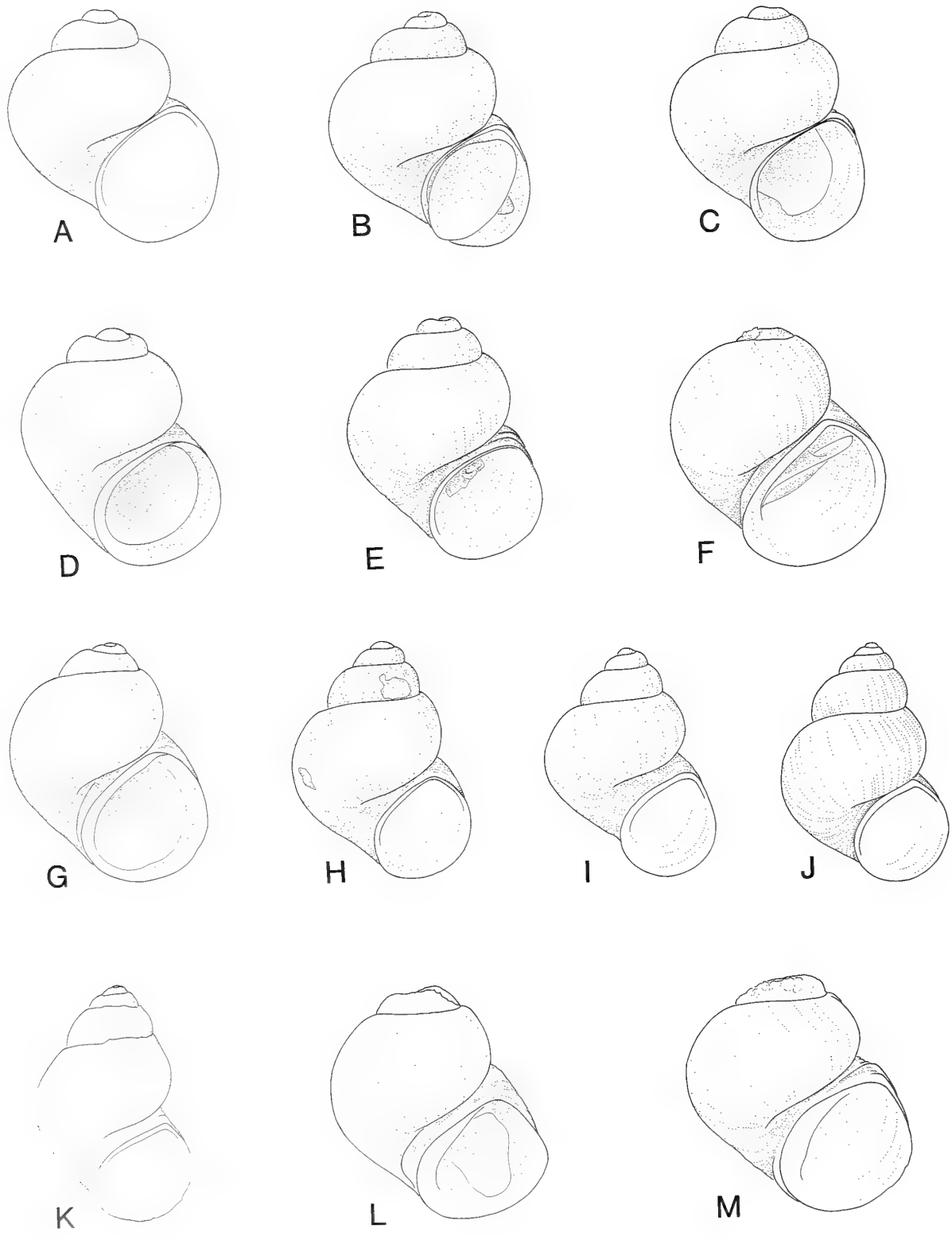
Pyrgulopsis avernalis (Pilsbry, 1935), Hershler, 1994:19, 21 [figures; transfer to *Pyrgulopsis*].

Diagnosis: Medium-sized, with globose-trochoid shell. Penis large, filament short, lobe absent. Penial ornament a large ventral gland.

Type locality: Colorado Desert (fossil); emended to Moapa Valley (southern Nevada) by Hershler (1994:19).

Remarks: All material collected during this survey was from the type locality area in Moapa Valley (Figure 49).

Material examined: NEVADA. *Clark County:* Spring,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Moapa National Wildlife Refuge, Moapa Valley, T. 14 S, R. 65 E, NE ¼ section 21, USNM 873454, USNM 874088, USNM 874344.—"Apcar Springs," Moapa Valley, T. 14 S, R. 65 E, SE ¼ section 16, USNM 874000, USNM 874014.—"Cardy Lamb Spring," Moapa Valley, T. 14 S, R. 65 E, SW ¼ section 16, USNM 874353, USNM 874354, USNM 874780, USNM 874781.—Springs, west of Muddy Spring, Moapa Valley, T. 14 S, R. 65 E, NW ¼ section 16, USNM 874003, USNM 874005, USNM 874015, USNM 874082, USNM 874089.—Muddy Spring, T. 14 S, R. 65 E, NE ¼ section 16, USNM 874110, USNM 874347.

Pyrgulopsis carinifera (Pilsbry, 1935)

Fluminicola avernalis carinifera Pilsbry, 1935:93, fig. 3.
"*Fluminicola*" *carinifera* Pilsbry, 1935, Taylor, 1975:53 [literature compilation].
"Undescribed species of *Fontelicella*" Pratt, 1977:7 [habitat notes].
Pyrgulopsis carinifera (Pilsbry, 1935), Hershler, 1994:26–27 [figures; transfer to *Pyrgulopsis*; elevation to full species status].

Diagnosis: Medium-sized, with trochoid shell. Penis medium-sized; filament medium length, lobe medium length. Penial ornament a large, fragmented terminal gland.

Type locality: Colorado Desert (fossil); emended to Moapa Valley (southern Nevada) by Hershler (1994:19).

Remarks: All material collected during this survey was from the type locality area in Moapa Valley (Figure 49).

Material examined: NEVADA. *Clark County:* Spring, Moapa National Wildlife Refuge, Moapa Valley, T. 14 S, R. 65 E, NE ¼ section 21, USNM 873475, USNM 874083, USNM 874097, USNM 874098, USNM 874507, USNM 874784, USNM 874785.—"Apcar Springs," Moapa Valley, T. 14 S, R. 65 E, SE ¼ section 16, USNM 874001, USNM 874004, USNM 874348.—Springs, west of Muddy Spring, Moapa Valley, T. 14 S, R. 65 E, NW ¼ section 16, USNM 874350.—Muddy Spring, T. 14 S, R. 65 E, NE ¼ section 16, USNM 874099, USNM 874111, USNM 874345, USNM 874786, USNM 874791.

Pyrgulopsis merriami (Pilsbry & Beecher, 1892)

Fluminicola merriami Pilsbry & Beecher in Pilsbry, 1892: 143.-Williams et al., 1985:36 [in part; habitat notes].
"*Fluminicola*" *merriami* Pilsbry & Beecher in Pilsbry, 1892, Taylor, 1975:122 [literature compilation].
Pyrgulopsis merriami (Pilsbry and Beecher in Pilsbry, 1892), Hershler, 1994:49 [figures; transfer to *Pyrgulopsis*].

Diagnosis: Medium-sized, with globose shell. Penis large, filament short, lobe medium length. Penial ornament a small terminal gland, large, trifid, penial gland; small Dg3, and large ventral gland.

Type locality: A warm spring in Pahranagat Valley, Nevada.

Remarks: This species occupies much of the upper course of the pluvial White River (Figure 49). Populations from the White River Valley differ from those of Pahranagat Valley in that the ventral gland of the penis is borne on a long stalk.

Material examined: NEVADA. *Nye County:* Hot Creek Spring, White River Valley, T. 6 N, R. 61 E, NE ¼ section 18, USNM 873159, USNM 874013, USNM 874689.—Moon River Spring, White River Valley, T. 6 N, R. 60 E, NE ¼ section 25, USNM 874677.—Moorman Spring, White River Valley, T. 8 N, R. 61 E, SE ¼ section 32, USNM 873190, USNM 874684.

Pyrgulopsis ***montana*** Hershler, sp. nov.

Camp Valley pyrg

(Figures 6D, 11B, 12B, 17E, 27C–E)

Etymology: From *montanus* (Latin), of mountains; referring to the montane habitat of this species.

Diagnosis: Medium-sized, with sub-globose to ovate-conic shell. Penis small, filament medium length, lobe short. Penial ornament a small terminal gland.

Description: Shell (Figures 6D, 17E) sub-globose to ovate-conic, width/height, 70–82%; height, 2.1–3.0 mm; width, 1.6–2.1 mm; whorls, 3.25–4.0. Protoconch (Figure 11B) 1.2 whorls, diameter 0.28 mm, smooth. Teleoconch whorls highly convex, sometimes having narrow shoulders. Aperture ovate, narrowly adnate or slightly separated from body whorl. Inner lip slightly thickened, without columellar shelf. Outer lip slightly thickened, weakly prosocline, without sinuation. Umbilicus perforate. Periostracum light brown.

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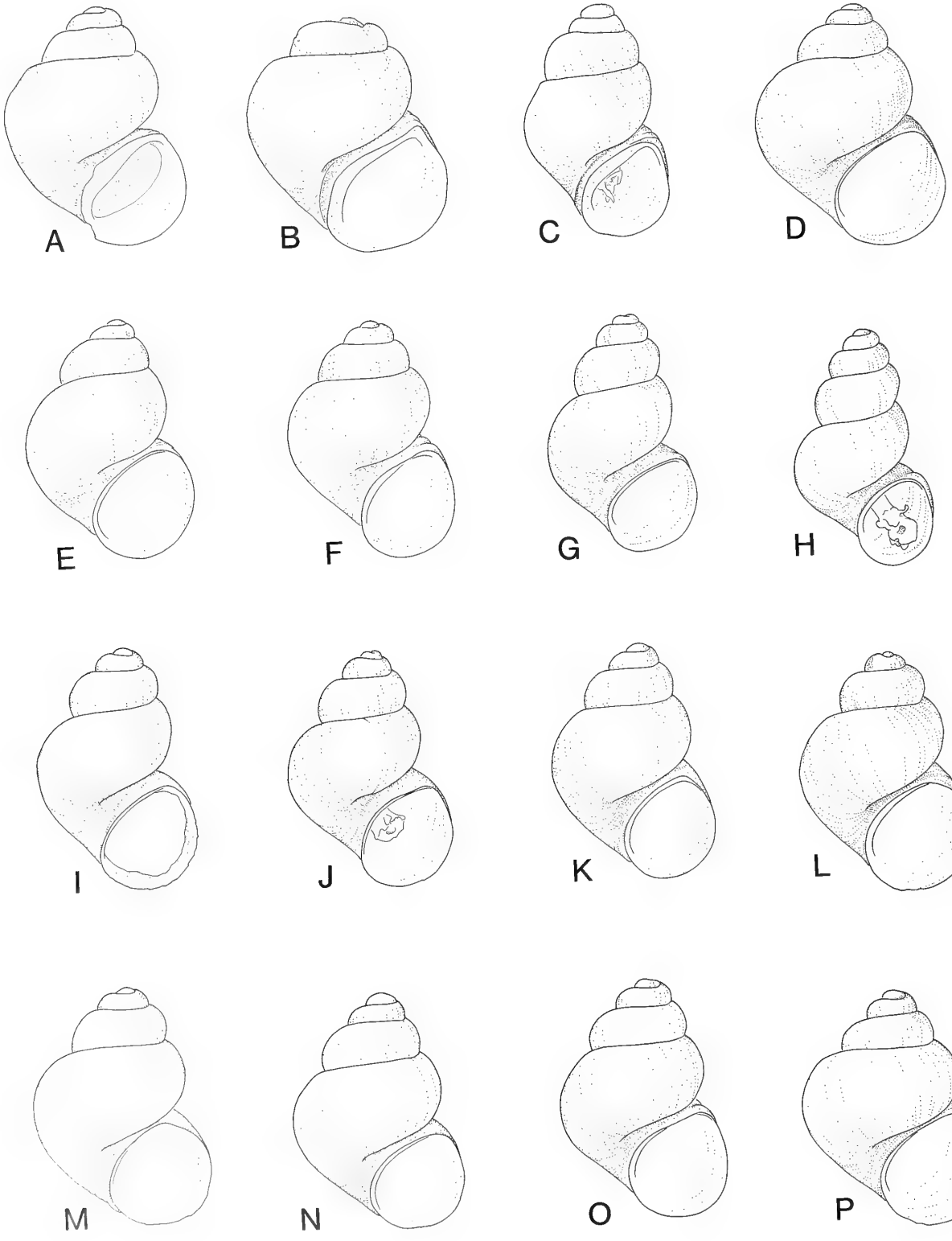
Figure 17

Shells of *Pyrgulopsis* species. A. *P.* ***fausta,*** holotype, USNM 874757 (shell height, 1.6 mm). B. *P.* ***deaconi,*** holotype, USNM 874454 (1.9 mm). C. *P.* ***deaconi,*** USNM 854737 (1.7 mm). D. *P.* ***coloradensis,*** holotype, USNM 854621 (1.2 mm). E. *P.* ***montana,*** holotype, USNM 874686 (1.8 mm). F. *P.* ***hubbsi,*** holotype, USNM 873415 (3.6 mm). G. *P.* ***hubbsi,*** USNM 873405 (3.0 mm). H. *P.* ***sathos,*** holotype, USNM 874664 (3.6 mm). I. *P.* ***sathos,*** USNM 874663 (2.1 mm). J. *P.* ***sathos,*** USNM 873198 (4.3 mm). K. *P.* ***sathos,*** USNM 883852 (4.2 mm). L. *P.* ***breviloba,*** holotype, USNM 873174 (1.9 mm). M. *P.* ***breviloba,*** USNM 874671 (1.3 mm).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Operculum (Figure 12B) ovate, dark amber, nuclear region reddish; nucleus eccentric; dorsal surface smooth; outer margin having weak rim. Attachment scar margin thick between nucleus and inner edge.

Radula 630 × 108 μm, with 55 rows of teeth. Central tooth 23 μm wide, with medium indented dorsal edge; lateral cusps, 6–7; central cusp narrow, daggerlike; basal cusps small. Basal process V-shaped, basal sockets medium depth. Lateral tooth formula 4(5)-1-4(5); neck medium flexed; outer wing 150% of cutting edge length. Inner marginal teeth with 27–30 cusps; cutting edge occupying 33% of tooth length. Outer marginal teeth with 30–31 cusps; cutting edge occupying 24% of tooth length. Stomach slightly longer than style sac; stomach chambers equal in size; stomach caecum very small.

Cephalic tentacles, snout, neck light to dark grey-brown. Foot light to dark grey, pigment heaviest along anterior and posterior margins. Opercular lobe medium to dark grey, pigment heaviest along inner edge and sides. Pallial roof, visceral coil near uniform medium to dark brown-grey or black. Dark internal pigment filling most of penial filament and portion of proximal penis; lobe also sometimes having scattered black pigment.

Ctenidial filaments, 17, pleated; ctenidium slightly overlapping pericardium posteriorly. Osphradium small, narrow, positioned alongside posterior half of ctenidium. Renal gland longitudinal-slightly oblique; kidney opening grey-white. Rectum broadly overlapping pallial oviduct, abutting prostate gland.

Ovary 0.5–0.75 whorl, filling 50% of digestive gland behind stomach, overlapping both stomach chambers. Distal female genitalia shown in Figure 27C. Albumen gland having medium pallial component. Capsule gland shorter, slightly narrower than albumen gland, broadly ovate in section; rectal furrow weakly developed. Ventral channel moderately overlapping capsule gland; longitudinal fold moderately developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a tight circular loop usually preceded by weak twist. Oviduct and bursal duct joining just behind pallial wall. Bursa copulatrix medium length and width, narrow-ovate, often having silvery appearance, longitudinal or oblique, positioned along postero-ventral edge of albumen gland, with small portion extending posterior to gland. Bursal duct originating from anterior edge at mid-line, long, medium width, broadening distally. Seminal receptacle small, pouchlike, overlapping or abutting proximal portion of bursal duct close to ventral edge of albumen gland.

Testis 1.25–1.5 whorls, filling 50% of digestive gland behind stomach, overlapping both stomach chambers anteriorly. Prostate gland small, broadly ovate, entirely visceral or having short pallial portion, narrowly ovate in section. Proximal pallial vas deferens straight or with weak undulation. Penis (Figure 27D, E) small; base rectangular to near square, strongly folded; filament slightly shorter than base, broad, tapering to sharp point, longitudinal; lobe short, knoblike, longitudinal. Terminal gland short, narrow-circular, sometimes longitudinal, ventral. Penial duct straight, near outer edge.

Type locality: Spring, upper Camp Valley, Lincoln County, Nevada, T. 5 N, R. 69 E, center section 8 (Figure 49). Holotype, USNM 874686 (Figure 17E), collected by R. Hershler and P. Hovingh, 24 June 1992; paratypes, USNM 860694. The type locality is a small rheocrene heavily impacted by cattle.

Remarks: This species closely resembles *P.* ***hamlinensis*** (described below), which occurs to the east in the Bonneville Basin, as both species share a smooth protoconch and relatively simple penis ornamented solely by a terminal gland. *Pyrgulopsis* ***montana*** differs from this species in its slightly broader shell with simple whorl outline, and weaker operculum attachment scar.

Material examined: NEVADA. *Lincoln County:* Spring, upper Camp Valley, USNM 860694, USNM 874686.

Pyrgulopsis ***hubbsi*** Hershler, sp. nov.

Hubbs pyrg

(Figures 6E, 14A–C, 17F, G, 27F–H)

Etymology: Named after the late Carl Hubbs, in recognition of his extensive contributions to the study of fishes and drainage history of the Great Basin.

Diagnosis: Medium-sized to large, with globose to low-conical shell. Penis medium-sized, filament long, lobe short. Penial ornament a dotlike terminal gland.

Description: Shell (Figures 6E, 17F, G) globose to low-conical, apex usually eroded, width/height, 82–95%;

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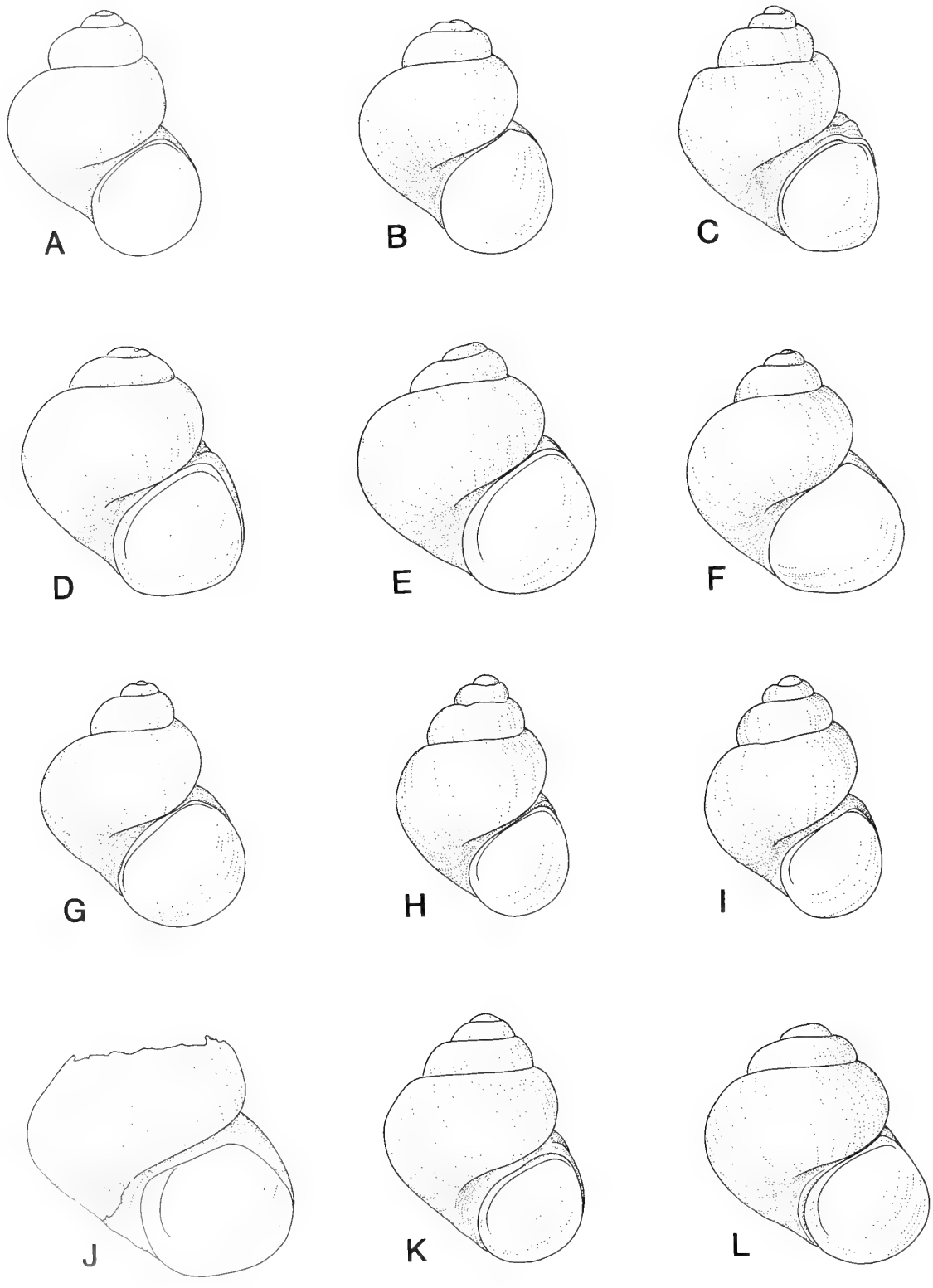
Figure 18

Shells of *Pyrgulopsis* species. A. *P.* ***lata,*** holotype, USNM 874667 (shell height, 1.9 mm). B. *P.* ***gracilis,*** holotype, USNM 873158 (2.0 mm). C. *P.* ***gracilis,*** USNM 883885 (2.1 mm). D. *P.* ***marcida,*** holotype, USNM 873154 (3.3. mm). E. *P.* ***marcida,*** USNM 874682 (3.9 mm). F. *P.* ***marcida,*** USNM 873170 (2.5 mm). G. *P.* ***turbatrix,*** holotype, USNM 883978 (2.9 mm). H. *P.* ***turbatrix,*** USNM 854738 (3.4 mm). I. *P.* ***turbatrix,*** USNM 874455 (2.5 mm). J. *P.* ***turbatrix,*** USNM 874775 (3.1 mm). K. *P.* ***sterilis,*** holotype, USNM 874876 (3.1 mm). L. *P.* ***sterilis,*** USNM 874769 (2.6 mm). M. *P.* ***ruinosa,*** holotype, USNM 873407 (2.6 mm). N. *P.* ***sublata,*** holotype, USNM 874681 (2.9 mm). O, P. *P.* ***sublata,*** USNM 860724 (2.2 mm, 2.4 mm, respectively).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height, 2.5–3.8 mm; width, 2.2–3.4 mm; whorls, 3.25–3.75. Protoconch 1.3 whorls, diameter 0.33 mm, initial 0.25 whorl finely wrinkled, later portion near smooth. Teleoconch whorls moderately convex, shoulders absent to well developed. Aperture broad, crescentlike, often strongly angled above; adnate or, less commonly, slightly disjunct. Inner lip thick, with medium width columellar shelf. Outer lip thick in larger specimens, prosocline, weakly sinuate. Umbilicus absent or rimate; umbilical region often weakly excavated with slight adaxial ridge. Periostracum light brown, thick.

Operculum ovate, amber, nuclear region reddish; nucleus eccentric; dorsal surface weakly frilled, outer margin having weak rim. Attachment scar slightly thickened between nucleus and inner edge.

Radula (Figure 14A–C) 1.19 × 140 μm, with 78 rows of teeth. Central tooth 40 μm wide, with slightly indented dorsal edge; lateral cusps, 4–6; central cusp long, medium width, daggerlike; basal cusps small. Basal tongue broad, nearly U-shaped, considerably shorter than lateral margins; basal sockets medium depth. Lateral tooth formula 2(3)-1-3(4); neck medium flexed; outer wing broad, 110% of cutting edge length. Inner marginal teeth with 21–24 cusps; cutting edge occupying 29% of length of tooth. Outer marginal teeth with 30–31 cusps; cutting edge occupying 30% of length of tooth. Stomach and style sac equal-sized; anterior and posterior stomach chambers equal-sized; stomach caecum absent or very small.

Cephalic tentacles light to dark brown, usually lighter centrally and around eyespots. Snout light to dark brown, usually darker than tentacles. Foot light to dark brown. Opercular lobe unpigmented to dark along inner edge and sides. Neck light to medium brown. Pallial roof, visceral coil nearly uniform dark brown-black. Penial filament darkly pigmented internally for entire length except distalmost portion; pigment extending into distal portion of base.

Ctenidial filaments, 30, pleated, ctenidium overlapping pericardium posteriorly. Osphradium small, narrowly ovate, centrally positioned. Renal gland oblique; kidney opening grey-white. Rectum broadly overlapping pallial oviduct, slightly overlapping prostate gland.

Ovary 0.75–1.0 whorl, filling more than 50% of digestive gland behind stomach, overlapping posterior and anterior stomach and extending to edge of albumen gland. Distal female genitalia shown in Figure 27F. Albumen gland having short pallial component. Capsule gland slightly shorter and narrower than albumen gland, subcircular in section; rectal furrow well developed. Ventral channel slightly overlapping capsule gland, longitudinal fold weakly developed. Genital aperture a terminal slit with short anterior extension. Coiled oviduct a tight circular loop preceded and overlapped by posterior arched kink or twist. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copulatrix short, medium width; sub-globular to broadly ovate, longitudinal, with 50–75% of length posterior to gland, anteriormost portion usually embedded in gland. Bursal duct originating from anterior edge at mid-line, long, narrow, embedded in albumen gland except for distalmost portion. Seminal receptacle small, pouchlike, positioned well anterior to bursa near ventral edge of albumen gland.

Testis 1.0 whorl, filling almost all of digestive gland behind stomach, overlapping anterior and posterior stomach chambers and extending to edge of prostate gland. Prostate gland very small, broadly ovate, entirely visceral or with short pallial component, narrowly ovate in section. Proximal pallial vas deferens straight. Penis (Figure 27G, H) medium-sized; base rectangular, weakly folded along inner edge; filament as long or slightly longer than base, broad, tapering, longitudinal; lobe very short, budlike, longitudinal. Terminal gland dotlike, circular, sometimes divided into two units, ventral. Penial duct weakly undulating in base, straight in filament, near outer edge.

Type locality: Hiko Spring, Pahranagat Valley, Lincoln County, Nevada, T. 4 S, R. 60 E, SE ¼ section 14. Holotype, USNM 873415 (Figure 17F), collected by R. Hershler, 9 July 1986; paratypes, USNM 860690. The type locality is a large, thermal (27°C.) rheocrene.

Remarks: *Pyrgulopsis* ***hubbsi*** resembles *P.* ***sathos*** (described next), from White River Valley, in having weak protoconch sculpture; short, broad lateral wings on the lateral marginal teeth; ovate bursa copulatrix with long duct; very small, anteriorly positioned seminal receptacle; and penis with enlarged filament, very small penial lobe, and small terminal gland. *Pyrgulopsis* ***hubbsi*** differs from this species in having a squatter shell, and lacking a ven-

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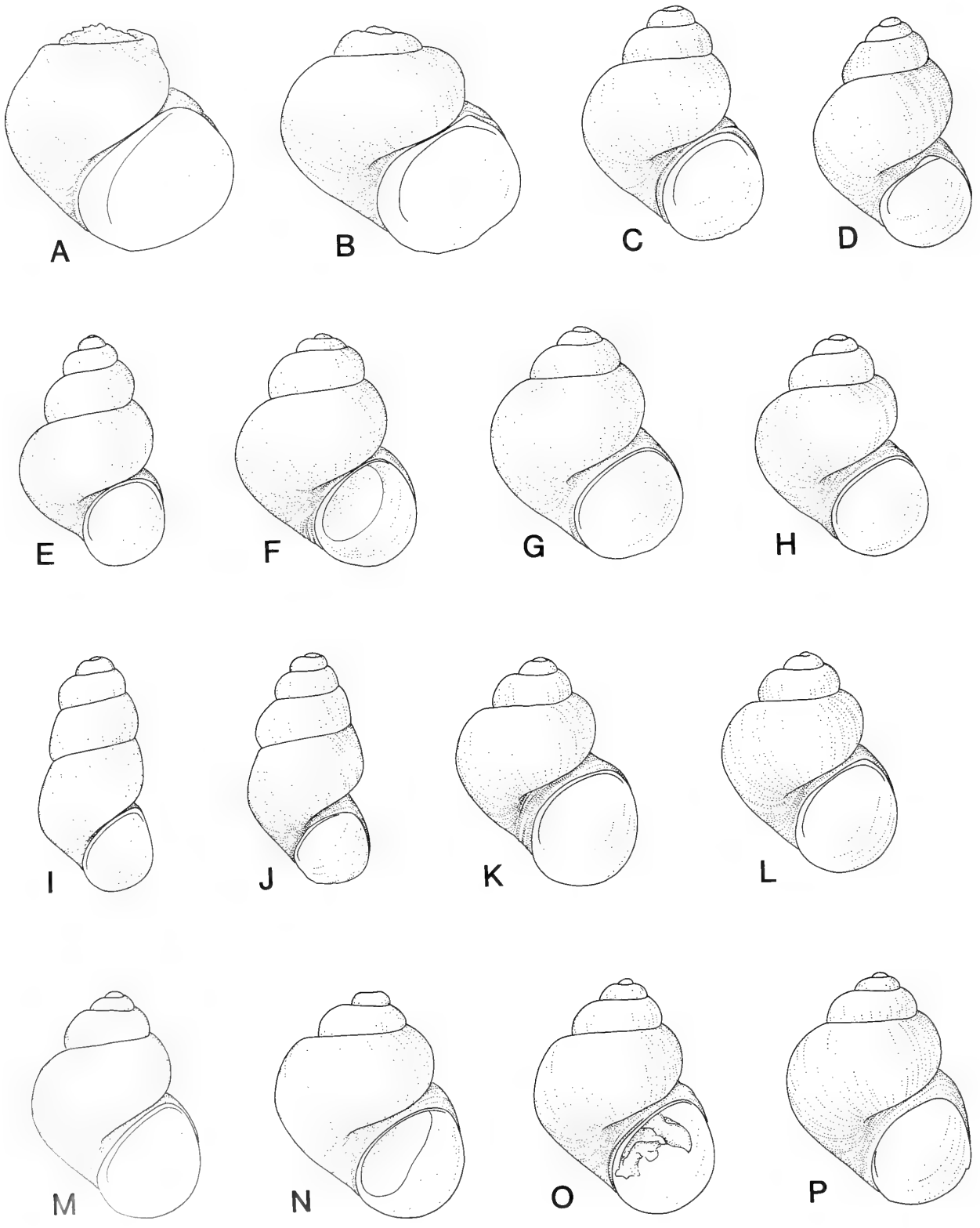
Figure 19

Shells of *Pyrgulopsis* species. A. *P.* ***lockensis,*** holotype, USNM 874779 (shell height, 2.0 mm). B. *P.* ***papillata,*** holotype, USNM 873185 (2.1 mm). C. *P.* ***carinata,*** holotype, USNM 883975 (2.2 mm). D. *P.* ***aloba,*** holotype, USNM 883847 (1.1 mm). E. *P.* ***aloba,*** USNM 873187 (1.3 mm). F. *P.* ***villacampae,*** holotype, USNM 873191 (2.6 mm). G. *P.* ***villacampae,*** USNM 883938 (3.6 mm). H. *P.* ***anatina,*** holotype, USNM 883848 (2.8 mm). I. *P.* ***anatina,*** USNM 860710 (2.5 mm). J. *P.* ***planulata,*** holotype, USNM 892023 (1.2 mm). K. *P.* ***sulcata,*** holotype, USNM 874326 (1.6 mm). L. *P.* ***orbiculata,*** holotype, USNM 873196 (1.3 mm).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tral gland on the penis. Distribution of *P. **hubbsi*** is shown in Figure 49.

Material examined: NEVADA. *Lincoln County:* Hiko Spring, USNM 860690, USNM 873166, USNM 873399, USNM 873415, USNM 874776.—Crystal Spring, Pahranagat Valley, T. 5 S, R. 60 E, NE ¼ section 10, USNM 873173, USNM 873404, USNM 873405, USNM 874081, USNM 874770.

*Pyrgulopsis **sathos*** Hershler, sp. nov.

White River Valley pyrg

(Figures 6F, 12C, 17H–K, 28A–C)

Etymology: From *sathon* (Greek), one with large penis; referring to the enlarged penial filament characterizing this species.

Diagnosis: Usually large, with ovate to narrow-conic shell. Penis medium-sized, filament long, lobe short. Penial ornament of small terminal and ventral glands.

Description: Shell (Figures 6F, 17H–K) ovate- to narrow-conic, width/height, 67–91%; height, 1.4–4.6 mm; width, 1.2–3.5 mm; whorls, 3.25–5.25. Protoconch 1.25 whorls, diameter 0.33 mm, weakly wrinkled along inner edge at apex, otherwise smooth. Teleoconch whorls medium to highly convex; shoulders absent or narrow. Aperture ovate, narrow adnate or slightly separated from body whorl. Inner lip slightly thickened, sometimes having very narrow columellar shelf. Outer lip thin, prosocline, without sinuation. Umbilicus perforate. Periostracum tan-brown.

Operculum (Figure 12C) ovate, reddish; nucleus slightly eccentric; dorsal surface weakly frilled; outer margin having well-developed rim. Attachment scar thick almost all around (except for section along outer edge).

Radula 890 × 150 μm, with 56 rows of teeth. Central tooth 39 μm wide, with slightly indented dorsal edge; lateral cusps, 4–5, central cusp medium width, dagger-like; basal cusps medium-sized, sometimes accompanied by vestige of second, outer cusp. Basal tongue broad V-shaped, shorter than lateral margins, basal sockets medium depth. Lateral tooth formula 2(3)-1-3(4); neck medium flexed; outer wing 150–170% of cutting edge length, broad. Inner marginal teeth with 21–26 cusps; cutting edge occupying 36% of length of tooth. Outer marginal teeth with 31–35 cusps; cutting edge occupying 25% of length of tooth. Stomach slightly longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum medium-sized.

Cephalic tentacles unpigmented to dark brown. Snout, foot light to dark brown. Opercular lobe usually dark along sides and inner edge. Neck unpigmented to medium brown. Pallial roof, visceral coil near uniform dark brown-black. Penial filament darkly pigmented internally along almost entire length.

Ctenidial filaments, 20, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, centered slightly posterior to middle of ctenidium. Renal gland strongly oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.75 whorl, filling 50% of digestive gland behind stomach, abutting or very slightly overlapping posterior stomach chamber. Distal female genitalia shown in Figure 28A. Albumen gland having short pallial component. Capsule gland shorter and narrower than albumen gland, ovate in section; rectal furrow weakly developed. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit, sometimes slightly raised and papillalike, with short anterior extension. Coiled oviduct of two small, overlapping posterior loops. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copulatrix short, slightly narrower than albumen gland, ovate, longitudinal, with 50% of length posterior to gland. Bursal duct originating from anterior edge of bursa at mid-line, as long or slightly shorter than bursa, ventral edge sometimes embedded in albumen gland. Seminal receptacle very small, pouchlike, positioned well anterior to bursa near ventral edge of albumen gland.

Testis 2.0 whorls, filling almost all of digestive gland behind stomach, overlapping posterior and part of anterior stomach chamber. Prostate gland bean-shaped, with short pallial portion, narrowly ovate in section. Proximal pallial vas deferens straight. Penis (Figure 28B, C) medium-sized; base rectangular, sometimes weakly folded along inner edge basally; filament as long or longer than base, broad, tapering to point, slightly oblique; lobe short, knoblike (sometimes quite narrow), oblique. Terminal gland short, sub-circular, transverse, ventral. Ventral

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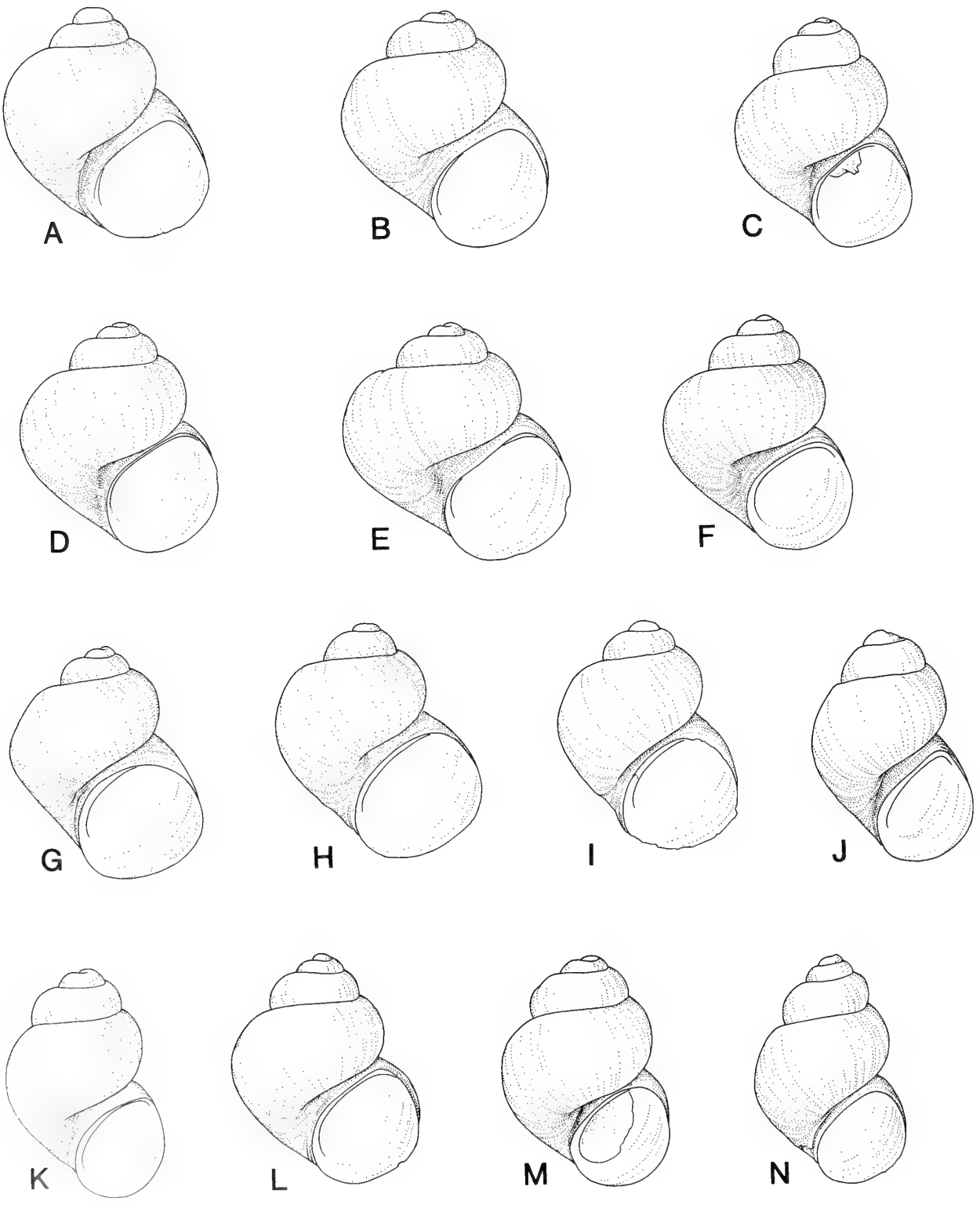
Figure 20

Shells of *Pyrgulopsis* species. A. *P. **neritella,*** holotype, USNM 883932 (shell height, 1.3 mm). B. *P. **landyei,*** holotype, USNM 892014 (1.4 mm). C. *P. **serrata,*** holotype, USNM 874314 (2.2 mm). D. *P. **serrata,*** USNM 874318 (2.5 mm). E. *P. **serrata,*** USNM 874312 (3.3 mm). F. *P. **cruciglans,*** holotype, USNM 874285 (1.9 mm). G. *P. **cruciglans,*** USNM 874335 (2.3 mm). H. *P. **cruciglans,*** USNM 874331 (2.2 mm). I. *P. **dixensis,*** holotype, USNM 874391 (1.8 mm). J. *P. **dixensis,*** USNM 860688 (1.8 mm). K. *P. **aurata,*** holotype, USNM 874393 (2.7 mm). L. *P. **aurata,*** USNM 860696 (2.4 mm). M. *P. **longiglans,*** holotype, USNM 873409 (2.3 mm). N. *P. **longiglans,*** USNM 883451 (1.4 mm). O. *P. **longiglans,*** USNM 883436 (2.1 mm). P. *P. **longiglans,*** USNM 874293 (2.0 mm).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gland similarly small and circular; borne on swelling, sometimes pronounced so that distal lobe has forklike appearance; positioned near outer edge distally. Penial duct straight, positioned very close to outer edge.

Type locality: Flag Springs, White River Valley, Nye County, Nevada, T. 7 N, R. 62 E, NE ¼ section 33. Holotype, USNM 874664 (Figure 17H), collected by R. Hershler and P. Hovingh, 28 June 1992; paratypes, USNM 860691. The type locality, the northernmost spring of the Flag Spring complex, is a large rheocrene (Figure 4A). Snails were collected on hard substrate in the pool just below the spring source.

Remarks: This species is compared with *P.* ***hubbsi*** above. The distribution of *P.* ***sathos*** is shown in Figure 49.

Material examined: NEVADA. *Nye County:* Flag Springs (north) (Figure 4A), USNM 860691, USNM 873165, USNM 874664, USNM 883856.—Flag Springs (middle), White River Valley, T. 7 N, R. 62 E, NW ¼ section 33, USNM 873179. *Lincoln County:* Camp Spring, White River Valley, T. 6 N, R. 60 E, NW ¼ section 36, USNM 874380, USNM 874663. *White Pine County:* Spring, Lund, White River Valley, T. 11 N, R. 62 E, NE ¼ section 4, USNM 874019, USNM 883591, USNM 883852.—Arnoldson Spring, White River Valley, T. 12 N, R. 61 E, SE ¼ section 12, USNM 874687.—Preston Big Spring, White River Valley, T. 12 N, R. 61 E, NE ¼ section 2, USNM 873198, USNM 874022, USNM 874673.

Pyrgulopsis ***breviloba*** Hershler, sp. nov.

Flag pyrg

(Figures 6G, 11C, 14D–F, 17L, M, 28D–F)

Etymology: From *brevis* (Latin), short, and *lobus,* projection; referring to the short penial lobe characterizing this species.

Diagnosis: Small, with low-trochoid shell. Penis large; filament medium length, distally bifid; lobe very short. Penial ornament a very small terminal gland.

Description: Shell (Figures 6G, 17L, M) low-trochoid, apex usually eroded; width/height, 77–105%; height, 1.2–2.2 mm; width, 1.0–2.0 mm; whorls 2.75–3.75. Protoconch (Figure 11C) 1.25 whorls, diameter 0.29 mm, weakly wrinkled along inner edge near apex (sculpture sometimes coalescing to form weak spiral elements), otherwise smooth. Teleoconch whorls medium convexity; strongly shouldered, sometimes strongly angulate near aperture. Aperture crescent-shaped, usually disjunct. Inner lip usually thick, having medium width columellar shelf. Outer lip slightly thickened, strongly prosocline, without sinuation. Umbilicus rimate or perforate; umbilical region sometimes well excavated with adaxial ridge. Periostracum light brown, thick.

Operculum narrowly ovate, amber, darker in nuclear region; nucleus eccentric; dorsal surface smooth or weakly frilled near inner edge; outer margin sometimes having weak rim. Attachment scar narrowly thickened between nucleus and inner edge.

Radula (Figure 14D–F) 667 × 110 μm, with 67 rows of teeth. Central tooth 21 μm wide, with highly indented dorsal edge; lateral cusps, 5–6, sometimes partly fused dorsally; central cusp broad, spoonlike; basal cusps small, sometimes flanked on inner side by weakly developed second cusp. Basal tongue broad V-shaped, slightly longer than lateral margins, basal sockets medium depth. Lateral tooth formula 3-1-4; neck weakly flexed; outer wing 370% of cutting edge length. Inner marginal teeth with 33–34 cusps; cutting edge 33% of length of tooth. Outer marginal teeth with 29–32 cusps; cutting edge 27% of length of tooth. Stomach and style sac equal in length; stomach chambers equal-sized; stomach caecum very small.

Cephalic tentacles medium to dark brown. Snout dark brown. Foot medium to dark brown, pigment usually heavier along anterior edge. Opercular lobe dark along inner edge, sometimes all around. Neck nearly unpigmented to dark. Pallial roof, visceral coil uniformly dark brown-black. Distal half of penis densely pigmented with internal grey granules.

Ctenidial filaments, 17, pleated; ctenidium abutting or slightly overlapping pericardium posteriorly. Osphradium small, narrow-ovate, centrally positioned. Renal gland longitudinal-oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

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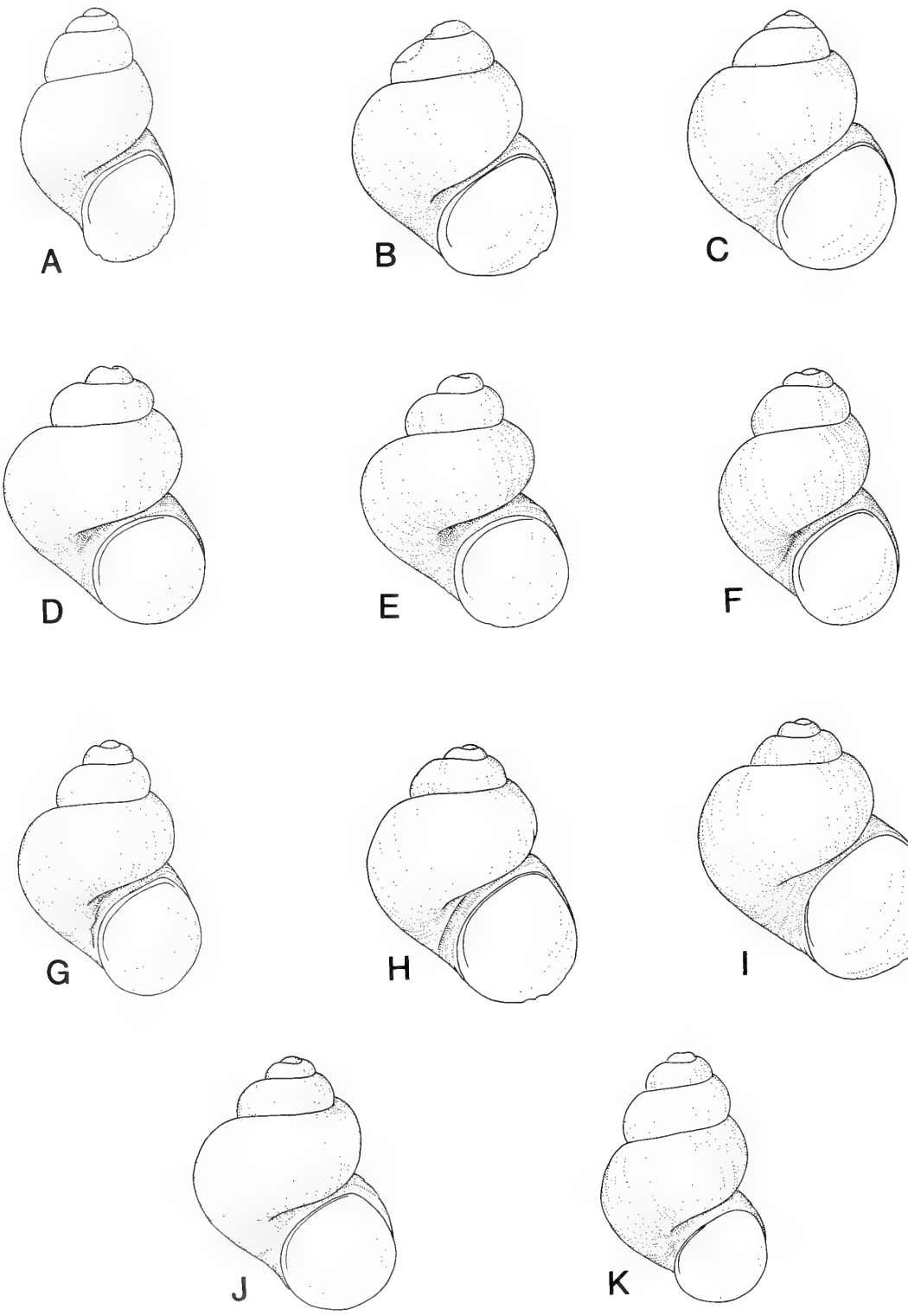
Figure 21

Shells of *Pyrgulopsis* species. A. *P.* ***militaris,*** holotype, USNM 873203 (shell height, 1.4 mm). B. *P.* ***militaris,*** USNM 883921 (1.6 mm). C. *P.* ***umbilicata,*** holotype, USNM 873208 (2.0 mm). D. *P.* ***umbilicata,*** USNM 873202 (2.0 mm). E. *P.* ***limaria,*** holotype, USNM 873232 (1.7 mm). F. *P.* ***limaria,*** USNM 874291 (2.0 mm). G. *P.* ***notidicola,*** holotype, USNM 873215 (2.0 mm). H. *P.* ***notidicola,*** USNM 874286 (1.7 mm). I. *P.* ***vinyardi,*** holotype, USNM 874740 (2.0 mm). J. *P.* ***imperialis,*** holotype, USNM 874207 (1.8 mm). K. *P.* ***imperialis,*** USNM 874211 (1.6 mm). L. *P.* ***sadai,*** holotype, USNM 874397 (2.5 mm). M. *P.* ***sadai,*** USNM 883900 (2.9 mm). N. *P.* ***sadai,*** USNM 883851 (3.0 mm).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Ovary a little more than 1.0 whorl, filling most of digestive gland behind stomach, overlapping posterior and part of anterior chambers anteriorly. Distal female genitalia shown in Figure 28D. Albumen gland having small-medium (16–30%) pallial component. Capsule gland slightly shorter and narrower than albumen gland, subcircular in section, rectal furrow pronounced. Ventral channel broadly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a broad circular loop preceded by a proximal twist. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, narrow or clublike, longitudinal, extending to edge of albumen gland. Bursal duct originating from anterior edge at mid-line, abutting oviduct; up to 50% length of bursa, medium width. Seminal receptacle small, narrow, overlapping anterior bursa along ventral edge, well anterior to edge of albumen gland.

Testis 1.5 whorls, filling more than 50% of digestive gland behind stomach, overlapping both stomach chambers anteriorly and abutting edge of prostate gland. Prostate broadly ovate, pallial portion medium, narrowly ovate in section. Proximal pallial vas deferens having sharp bend. Penis (Figure 28E, F) large; elongate-rectangular, base weakly folded along inner edge; filament medium length, rectangular, as wide as base, distally bifid; lobe extremely short, tapered, longitudinal. Terminal gland very small, circular, borne on ventral surface of lobe. Penial duct straight, near outer edge.

Type locality: Flag Springs, White River Valley, Nye County, Nevada, T. 7 N, R. 62 E, NE ¼ section 32. Holotype, USNM 873174 (Figure 17L), collected by J. J. Landye, 1 September 1973; paratypes, USNM 860689. Flag Springs comprises three springs draining to Sunnyside Creek, located within the Wayne Kirch Wildlife Management Area. The type locality, the middle of the three, nearly north-south trending springs; is a narrow rheocrene having a relatively large discharge.

Remarks: This snail and two other species from White River Valley, *P.* ***lata*** and *P.* ***gracilis*** (described next), share unusual features of strongly shouldered shell whorls, angular aperture, and well-developed columellar shelf. These species, which occur in closely adjacent spring complexes, are also closely similar in shape of central and lateral radular teeth, and configuration of distal female genitalia, but their penes are dissimilar, and that of *P.* ***breviloba*** is unique in its combination of elongate shape; very small lobe bearing weak terminal gland; and broadly rectangular, distally bifurcate filament. *Pyrgulopsis* ***bifurcata*** (described below), from Carico Lake Basin, also has a bifurcate penial filament, but has a completely different pattern of penial ornament than *P.* ***breviloba*** and also differs in various other features. The distribution of *P.* ***breviloba*** is shown in Figure 50.

Material examined: NEVADA. *Lincoln County:* Meloy Spring, Dry Lake Valley, T. 5 N, R. 65 E, NE ¼ section 32, USNM 874671. *Nye County:* Flag Springs (middle), USNM 860689, USNM 873174, USNM 883846.—Flag Springs (north), T. 7 N, R. 62 E, NE ¼ section 30, USNM 873188, USNM 874029, USNM 874031, USNM 883874.

Pyrgulopsis ***lata*** Hershler, sp. nov.

Butterfield pyrg

(Figures 6H, 12D, 18A, 29A–E)

Etymology: From *latus* (Latin), broad or wide; referring to the prominent columellar shelf characterizing shells of this species.

Diagnosis: Small, with ovate to narrow-conic shell. Penis large, filament short, lobe short. Penial ornament a small, fragmented terminal gland; very small Dg1, and small ventral gland.

Description: Shell (Figures 6H, 18A) ovate- to narrow-conic, apex usually eroded, width/height, 66–84%; height, 1.6–2.1 mm; width, 1.2–1.6 mm; whorls, 3.75–4.25. Protoconch 1.25 whorls, diameter 0.28 mm, early portion wrinkled along inner edge, otherwise smooth. Teleoconch whorls moderately convex, strongly shouldered; adapical region strongly angulate or keel-like; body whorl often slightly disjunct behind the aperture. Aperture ovate, angled above, usually disjunct, sometimes broadly so. Inner lip slightly thickened, having broad, well-developed columellar shelf. Outer lip slightly thickened, prosocline, without sinuation. Umbilicus perforate to broadly open. Periostracum light brown.

Operculum (Figure 12D) ovate, light amber, inner edge

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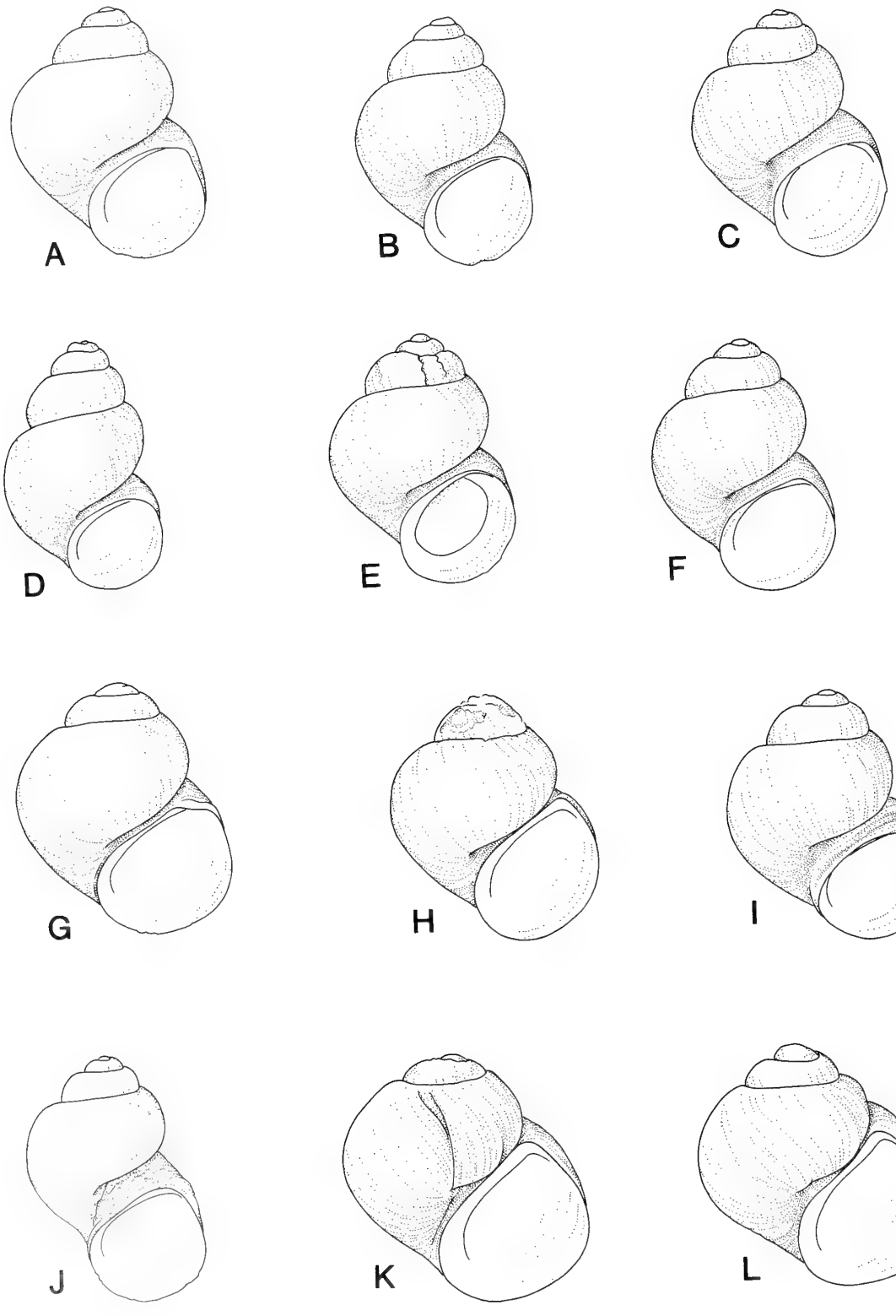
Figure 22

Shells of *Pyrgulopsis* species. A. *P.* ***augustae,*** holotype, USNM 874402 (shell height, 2.3 mm). B. *P.* ***pictilis,*** holotype, USNM 874401 (2.6 mm). C. *P.* ***pictilis,*** USNM 860713 (2.4 mm). D. *P.* ***basiglans,*** holotype, USNM 874280 (1.5 mm). E. *P.* ***bifurcata,*** holotype, USNM 874306 (1.3 mm). F. *P.* ***pellita,*** holotype, USNM 883850 (3.2 mm). G. *P.* ***leporina,*** holotype, USNM 874336 (2.9 mm). H. *P.* ***humboldtensis,*** holotype, USNM 874722 (2.2 mm). I. *P.* ***humboldtensis,*** USNM 874725 (2.5 mm). J. *P.* ***humboldtensis,*** USNM 874719 (2.5 mm). K. *P.* ***hamlinensis,*** holotype, USNM 883215 (2.0 mm).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straight, nucleus eccentric; dorsal surface smooth. Attachment scar slightly thickened between nucleus and inner edge.

Radula 575 × 85 μm, with 74 rows of teeth. Central tooth 17 μm wide, with highly indented dorsal edge; lateral cusps, 6–7 (often fused dorsally), central cusp medium width to broad, spoonlike; basal cusps medium-sized. Basal process V-shaped, basal sockets medium depth. Lateral tooth formula, 3(4)-1-5; neck weakly flexed; outer wing 257% of cutting edge length. Inner marginal teeth with 34–36 cusps; cutting edge occupying 36% of length of tooth. Outer marginal teeth with 31–34 cusps; cutting edge occupying 24% of length of tooth. Stomach longer than style sac, anterior chamber larger than posterior chamber; stomach caecum very small to nearly absent.

Cephalic tentacles light to dark grey-brown, sometimes lighter around eyespots and along narrow central zone. Snout medium to dark grey-brown. Foot, neck light to dark grey-brown. Opercular lobe dark along inner edge and sides, light-dark elsewhere. Pallial roof, visceral coil uniform black. Penial filament darkly pigmented internally for most of length.

Ctenidial filaments, 15, weakly pleated; ctenidium slightly overlapping pericardium posteriorly. Osphradium small, narrow, positioned centrally. Renal gland slightly oblique; kidney opening white. Rectum broadly overlapping genital ducts.

Ovary 1.0–1.25 whorls, filling 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 29A. Albumen gland having short pallial component. Capsule gland slightly shorter and narrower than albumen gland, subcircular in section; rectal furrow weakly developed. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a short, terminal slit often mounted on small raised swelling or papilla; anterior extension short. Coiled oviduct a circular loop usually preceded by small anterior twist or bend. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copulatrix considerably narrower and shorter than albumen gland, ovate, longitudinal or slightly oblique, less than 33% of length posterior to gland. Bursal duct originating from anterior edge near mid-line, medium length and width, slightly broader distally. Seminal receptacle small, pouchlike, overlapping or abutting ventral edge of anterior portion of bursa (a little dorsal to ventral edge of albumen gland).

Testis 1.0–1.25 whorls, filling 50% of digestive gland behind stomach, overlapping posterior stomach chamber anteriorly. Prostate gland bean-shaped, pallial portion short, narrow ovate in section. Proximal pallial vas deferens with undulation. Penis (Figure 29B-E) large, base rectangular, often elongate and expanded distally, weakly folded along inner edge; filament short, medium width, tapering to pointed tip, longitudinal or slightly oblique; lobe short to near absent, hemispherical, slightly oblique. Terminal gland small, usually divided into two to six small dotlike units along edge of lobe. Dg1 very small, rarely including a second, dotlike unit, borne on low swelling, near outer edge just proximal to filament. Ventral gland small, narrow, borne on low swelling, often curved into U-shape and extending near or onto edge of lobe, positioned near outer edge distally. Penial duct straight, near outer edge.

Type locality: Butterfield Springs, White River Valley, Nye County, Nevada, T. 7 N, R. 62 E, NE ¼ section 28 (Figure 50). Holotype, USNM 874667 (Figure 18A), collected by R. Hershler and P. Hovingh, 28 June 1992; paratypes, USNM 860697. The type locality is a small rheocrene.

Remarks: *Pyrgulopsis* ***lata*** differs from similarly shelled White River Valley species (see above) in having a very weak penial lobe; small, distal Dg1 (absent in the above); and large ventral gland (smaller in *P.* ***breviloba,*** absent in *P.* ***gracilis***). *Pyrgulopsis* ***lata*** resembles *P.* ***saxatilis*** (described below), from western Bonneville Basin, in penial form and ornament, but is readily distinguished by its narrower shell, fragmented terminal gland, larger bursa copulatrix with shorter duct, and more posteriorly positioned seminal receptacle.

Material examined: NEVADA. *Nye County:* Butterfield Springs, USNM 860697, USNM 873167, USNM 874667.

Pyrgulopsis ***gracilis*** Hershler, sp. nov.

Emigrant pyrg

(Figures 6I, 11D, 18B, C, 29F–H)

Etymology: From *gracilis* (Latin), slender; referring to the narrow penial filament characterizing this species.

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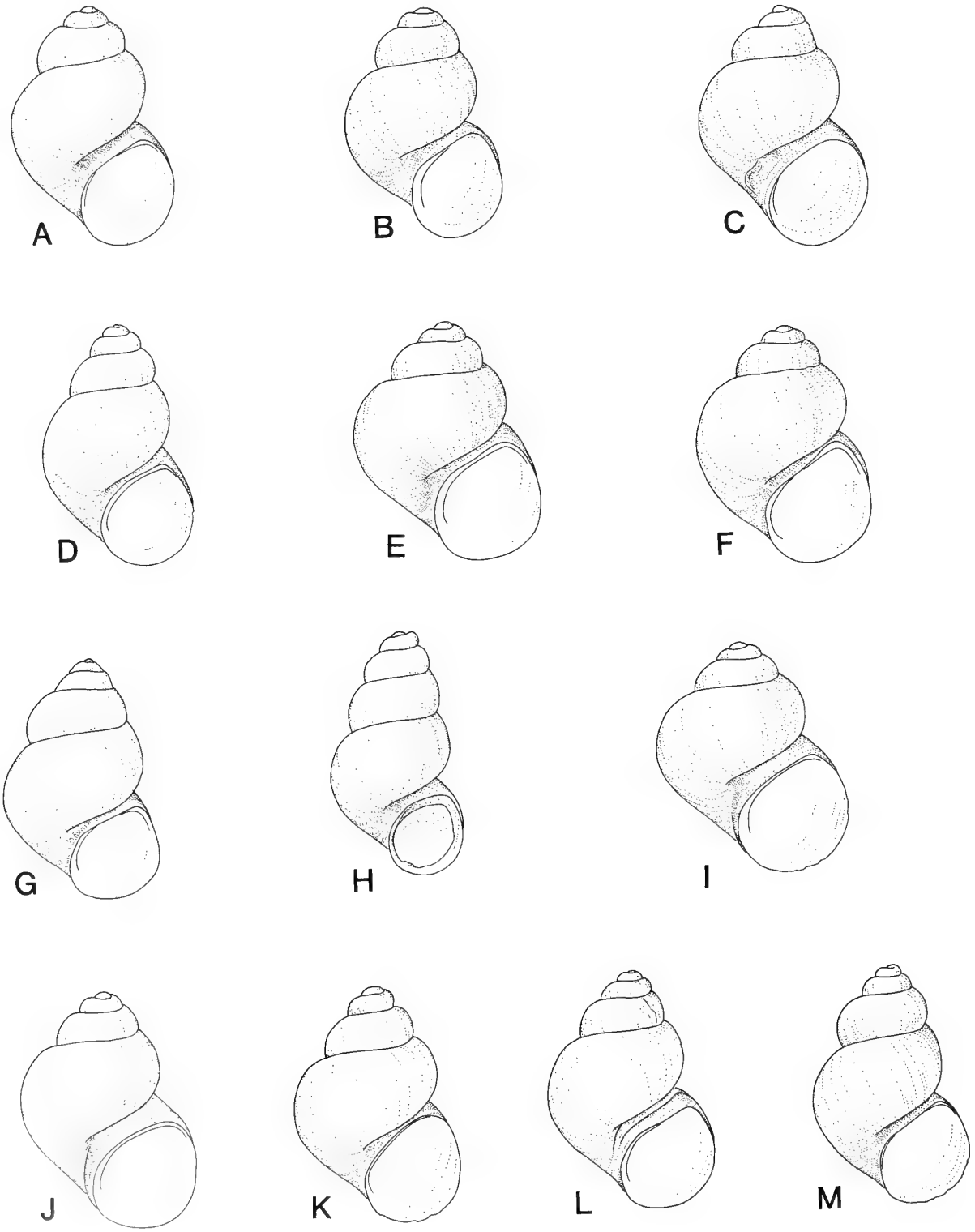
Figure 23

Shells of *Pyrgulopsis* species. A. *P.* ***peculiaris,*** holotype, USNM 883933 (shell height, 2.2 mm). B. *P.* ***peculiaris,*** USNM 883622 (2.8 mm). C. *P.* ***peculiaris,*** USNM 883603 (2.5 mm). D. *P.* ***peculiaris,*** USNM 874683 (2.5 mm). E. *P.* ***peculiaris,*** USNM 874319 (2.5 mm). F. *P.* ***peculiaris,*** USNM 883227 (2.2 mm). G. *P.* ***peculiaris,*** USNM 883222 (1.9 mm). H. *P.* ***anguina,*** holotype, USNM 874678 (2.3 mm). I, J. *P.* ***anguina,*** USNM 883205 (2.7 mm, 2.6 mm, respectively). K. *P.* ***saxatilis,*** holotype, USNM 883237 (1.3 mm). L. *P.* ***saxatilis,*** USNM 860726 (1.1 mm).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Diagnosis: Small, with broad- to narrow-conic shell. Penis medium-sized, filament long, lobe short or absent. Penial ornament a small terminal gland and large penial gland.

Description: Shell (Figures 6I, 18B, C) narrow conic, but apex usually highly eroded, producing a broadly conical shape; width/height, 81–92%; height, 1.6–1.9 mm; width, 1.3–1.6 mm; up to 4.0 whorls remaining. Protoconch (Figure 11D) 1.25 whorls, diameter 0.28 mm, initial 0.75 whorl finely wrinkled, later portion near smooth. Teleoconch whorls moderately convex, shoulders well developed, often forming a pronounced subsutural angulation on penultimate two whorls. Aperture ovate, well angled above, broadly adnate to slightly disjunct. Inner lip thick, with narrow columellar shelf. Outer lip thin-thick, prosocline, weakly sinuate. Umbilicus absent or rimate. Periostracum tan, brown, or reddish.

Operculum ovate, amber, darker in nuclear region; nucleus eccentric; dorsal surface smooth. Attachment scar margin slightly thickened between nucleus and inner edge, and along inner edge.

Radula 490 × 80 μm, with 60 rows of teeth. Central tooth 18 μm wide, with highly indented dorsal edge; lateral cusps, 5–6; central cusp medium width, spoonlike; basal cusps medium-sized. Basal process V-shaped, slightly longer than lateral margins, basal sockets medium depth. Lateral tooth formula 3(4)-1-4(5); neck weakly flexed; outer wing 215% of cutting edge length. Inner marginal teeth with 30–31 cusps; cutting edge occupying 35% of length of tooth. Outer marginal teeth with 27–31 cusps; cutting edge occupying 28% of length of tooth. Stomach slightly longer than style sac; stomach chambers equal-sized; stomach caecum very small.

Cephalic tentacles light to medium brown, often unpigmented around eyespots and along narrow central region. Snout medium to dark brown. Foot light to dark brown-black, especially dark along anterior edge. Opercular lobe usually medium brown, often slightly darker along sides. Neck nearly unpigmented to medium brown, often much lighter than rest of head. Pallial roof, visceral coil near uniform dark brown-black. Penial filament darkly pigmented internally.

Ctenidial filaments 19, weakly pleated; ctenidium slightly overlapping pericardium posteriorly. Osphradium small, narrow, positioned alongside posterior half of ctenidium. Renal gland oblique, sometimes strongly so; kidney opening grey-white. Rectum broadly overlapping pallial oviduct and slightly overlapping prostate gland.

Ovary 0.75 whorl, filling 50% of digestive gland behind stomach, partly overlapping posterior stomach chamber anteriorly. Distal female genitalia shown in Figure 29F. Albumen gland having short pallial component. Capsule gland slightly shorter and narrower than albumen gland, ovate in section; rectal furrow weak or absent. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a short terminal slit without anterior extension. Coiled oviduct a tight sub-circular coil preceded by weak posterior bend. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copulatrix medium length and width, ovate, longitudinal, with 50% of length posterior to gland. Bursal duct originating from anterior edge near mid-line, slightly shorter to slightly longer than bursa, medium width. Seminal receptacle short, narrow, overlapping or abutting proximal bursal duct, sometimes slightly overlapped by albumen gland.

Testis 1.25 whorls, filling almost all of digestive gland behind stomach, overlapping both stomach chambers anteriorly. Prostate gland bean-shaped, pallial section short, ovate in section. Proximal pallial vas deferens having weak undulation, almost straight. Penis (Figure 29G, H) medium-sized; base rectangular, folded along inner edge; filament as long as base, narrow, gently tapering, longitudinal; lobe short to almost absent, knoblike, longitudinal. Terminal gland small, sometimes very reduced, circular, sometimes divided into two to three dotlike units, usually ventral. Penial gland filling 50% of filament length, narrow, centrally positioned, usually bulging below inner edge of filament. Filament also sometimes bearing small, dotlike gland near base. Penial duct straight, near outer edge.

Type locality: Emigrant Springs, White River Valley, Nye County, Nevada, T. 9 N, R. 62 E, NE ¼ section 19 (Figure 50). Holotype, USNM 873158 (Figure 18B), collected by J. J. Landye, 2 September 1973; paratypes, USNM 860698. Emigrant Springs comprises a spring complex alongside Nevada State HWY 318. The type locality, the northernmost spring in this complex, is a small rheocrene.

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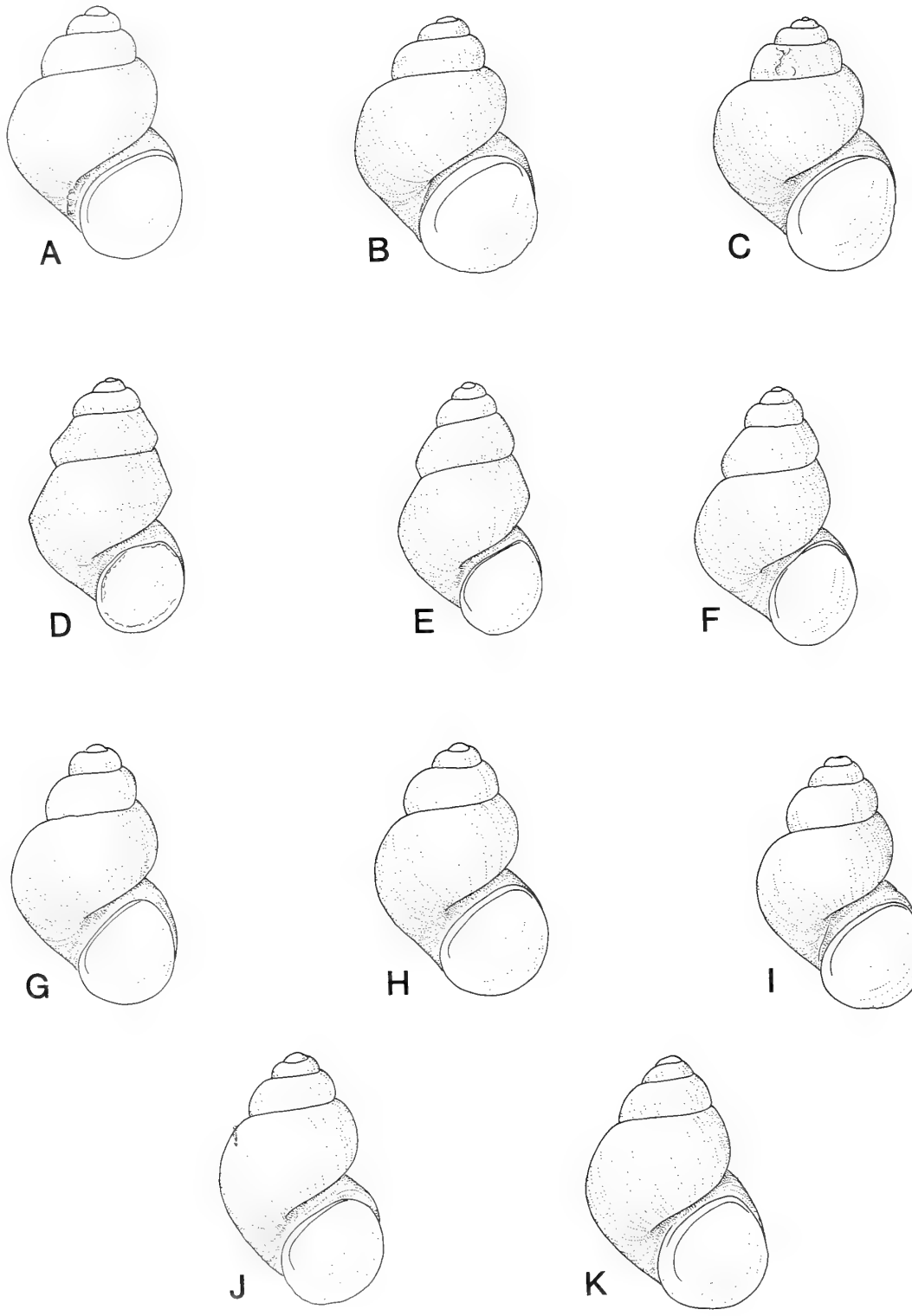
Figure 24

Shells of *Pyrgulopsis* species. A. ***P. variegata,*** holotype, USNM 883627 (shell height, 2.7 mm). B. ***P. variegata,*** USNM 883888 (2.5 mm). C. ***P. variegata,*** USNM 874713 (2.7 mm). D. ***P. variegata,*** USNM 883599 (3.1 mm). E. ***P. hovinghi,*** holotype, USNM 874075 (2.5 mm). F. ***P. millenaria,*** holotype, USNM 874720 (2.5 mm). G. ***P. lentiglans,*** holotype, USNM 874724 (1.8 mm). H. ***P. lentiglans,*** USNM 854540 (2.2 mm). I. ***P. plicata,*** holotype, USNM 883594 (2.5 mm). J. ***P. plicata,*** USNM 860727 (2.7 m). K. ***P. fusca,*** holotype, USNM 883439 (2.7 mm), L. ***P. fusca,*** USNM 883573 (3.3 mm). M. ***P. fusca,*** USNM 883442 (2.9 mm).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Remarks: This species has an unique penial morphology featuring a very slender filament with an elongate penial gland along its inner edge. Although *P. **gracilis*** otherwise resembles two other species found in White River Valley (see above), this snail is further distinguished by stronger protoconch microsculpture, unfused cusps on the central radular teeth, and the more posteriorly positioned bursa copulatrix.

Material examined: NEVADA. *Nye County:* Emigrant Springs (north), USNM 860698, USNM 873158, USNM 874382, USNM 883842.—Emigrant Springs (south), White River Valley (Figure 4B), T. 9 N, R. 62 E, NE ¼ section 30, USNM 883885.

*Pyrgulopsis **marcida*** Hershler, sp. nov.

Hardy pyrg

(Figures 6J, 18D–F, 30A–C)

Etymology: From *marcidus* (Latin), withered or wasted; referring to the reduced penial glands of this species.

Diagnosis: Small to medium-sized, with ovate- to elongate-conic shell. Penis medium-large; filament and lobe medium length. Penial ornament a small terminal gland, very small penial gland (sometimes absent), and occasional small gland on ventral surface of lobe.

Description: Shell (Figures 6J, 18D–F) ovate- to elongate conic, width/height, 66–86%; height, 1.6–3.9 mm; width, 1.2–3.0 mm; whorls, 3.5–4.75. Protoconch 1.25 whorls, diameter 0.35 mm, smooth. Teleoconch whorls moderately convex, shouldered, often having deep sutures; body whorl often slightly disjunct behind the aperture. Aperture ovate, narrowly adnate to slightly disjunct. Inner lip thin, without columellar shelf. Outer lip usually thin, orthocline or slightly prosocline, without sinuation. Umbilicus narrow-perforate. Periostracum tan.

Operculum ovate, amber, reddish in nuclear region; nucleus eccentric; dorsal surface frilled; outer margin having weak rim. Attachment scar thick (especially so along inner edge) all around.

Radula 687 × 119 μm, with 57 rows of teeth. Central tooth 28 μm wide, with medium indented dorsal edge; lateral cusps, 7–8; central cusp medium width, rounded; basal cusps small. Basal process V-shaped, basal sockets medium depth. Lateral tooth formula 4-1-5; neck well flexed; outer wing 215% of cutting edge length. Inner marginal teeth with 31–34 cusps; cutting edge occupying 33% of length of tooth. Outer marginal teeth with 37–39 cusps; cutting edge occupying 24% of length of tooth. Stomach slightly longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum medium-sized.

Cephalic tentacles very light grey-brown. Snout light to medium grey. Foot light to medium grey, darkest along anterior edge. Opercular lobe medium grey to black along anterior edge and sides, sometimes all around (central region lighter). Neck light to medium grey-brown. Pallial roof and visceral coil uniformly dark brown-black. Penial filament darkly pigmented internally.

Ctenidial filaments, 21, pleated; ctenidium slightly overlapping pericardium posteriorly. Osphradium small, narrow, positioned alongside posterior half of ctenidium. Renal gland slightly oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.5–0.75 whorl, filling less than 50% of digestive gland behind stomach, abutting or slightly overlapping posterior stomach chamber anteriorly. Distal female genitalia shown in Figure 30A. Albumen gland having short pallial component. Capsule gland as wide and slightly shorter to as long as albumen gland, sub-circular in section; rectal furrow deep. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct of two short, overlapping tight coils, usually posterior-oblique in orientation. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copulatrix medium length and width, ovate, usually longitudinal, with 33% or less of length posterior to gland. Bursal duct originating from anterior edge near mid-line, shorter than bursa, medium width. Seminal receptacle small, pouchlike, overlapping proximal bursal duct near ventral edge of albumen gland, often shallowly embedded in gland.

Testis 1.75–2.0 whorls, filling almost all of digestive gland behind stomach, overlapping posterior and small portion of anterior stomach chambers. Prostate gland bean-shaped, pallial portion short, narrowly ovate in section. Proximal pallial vas deferens having sharp, reflexed bend. Penis (Figure 30B, C) medium-large; base rectangular, sometimes weakly folded along inner edge; filament slightly shorter than base, medium width, tapering to point, near longitudinal to strongly oblique; lobe short,

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Figure 25

Shells of *Pyrgulopsis* species. A. *P. **chamberlini,*** holotype, USNM 883576 (2.8 mm). B, C. *P. **chamberlini,*** USNM 883944 (2.9 mm, 3.8 mm, respectively). D. *P. **inopinata,*** holotype, USNM 883943 (2.9 mm). E, F. *P. **inopinata,*** USNM 860730 (2.9 mm, 2.8 mm, respectively). G. *P. **nonaria,*** holotype, USNM 883566 (2.5 mm). H. *P. **transversa,*** holotype, USNM 883221 (2.3 mm). I. *P. **transversa,*** USNM 860732 (2.3 mm). J. *P. **transversa,*** USNM 883422 (2.4 mm). K. *P. **transversa,*** USNM 883597 (3.0 mm).

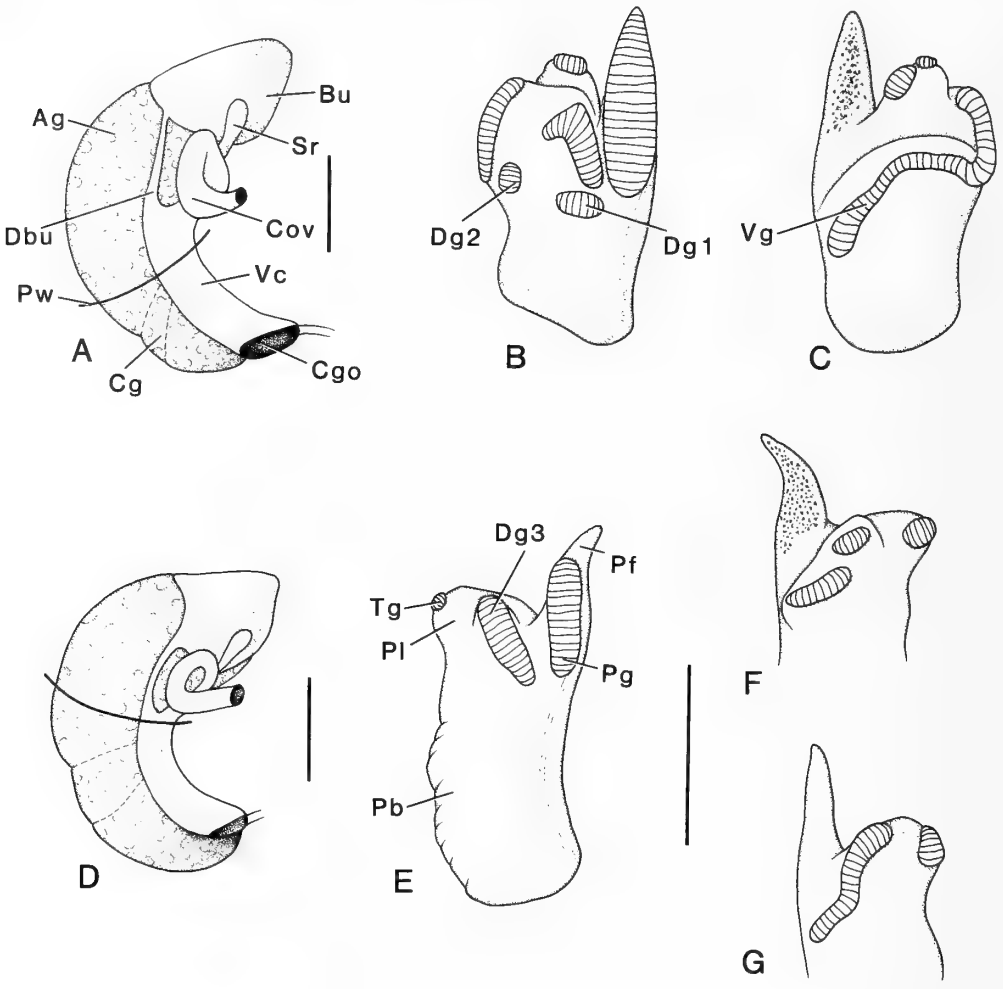


Figure 26

Genitalia of *Pyrgulopsis* species. (A–C, *P. **fausta,*** USNM 873175; D–G, *P. **deaconi,*** USNM 873355). A. Female glandular oviduct and associated structures, bar = 0.25 mm. B. Dorsal aspect of penis, scale as in A. C. Ventral aspect of penis, scale as in A. D. Female glandular oviduct and associated structures, bar = 0.25 mm. E. Dorsal aspect of penis, bar = 0.5 mm. F, G, Ventral aspect of distal penis, scale as in E. Ag = albumen gland, Bu = bursa copulatrix, Cg = capsule gland, Cgo = opening of capsule gland, Cov = coiled oviduct, Dbu = duct from bursa copulatrix, Dg1 = proximal dorsal gland on penis, Dg2 = dorsal gland near inner, distal edge of penis, Dg3 = dorsal gland near outer edge of penial lobe, Pb = base of penis, Pf = penial filament, Pg = gland on penial filament, Pl = lobe of penis, Pw = pallial wall, Sr = seminal receptacle, Vc = ventral channel of capsule gland, Vg = gland on ventral surface of penis.

sometimes near absent, knoblike, near longitudinal to oblique. Terminal gland small, narrow, variably oriented or reduced to two to three dotlike units, usually ventral. Penial gland very small, ovate, positioned near base of filament, often absent. Dotlike Dg2 rarely present along inner edge distally. Ventral lobe sometimes bearing small, often slightly raised gland proximally (adjacent to terminal gland) that may represent a reduced ventral gland. Penial duct straight, near outer edge.

Type locality: Hardy Springs, White River Valley, Nye County, Nevada, T. 9 N, R. 61 E, SW ¼ section 13. Holotype, USNM 873154 (Figure 18D), collected by J. J. Landye, 3 September 1973; paratypes, USNM 860711. The type locality is a small rheocrene.

Remarks: This species resembles *P. **anatina*** (described below), from Duckwater Valley, but differs in having a reflexed pallial vas deferens, squatter penis with shorter, broader lobe and filament; occasional presence of gland on ventral penis, smaller penial gland, narrower oviduct coil with two well-developed loops, and smaller seminal receptacle. Snails from Cave Valley have considerably lighter

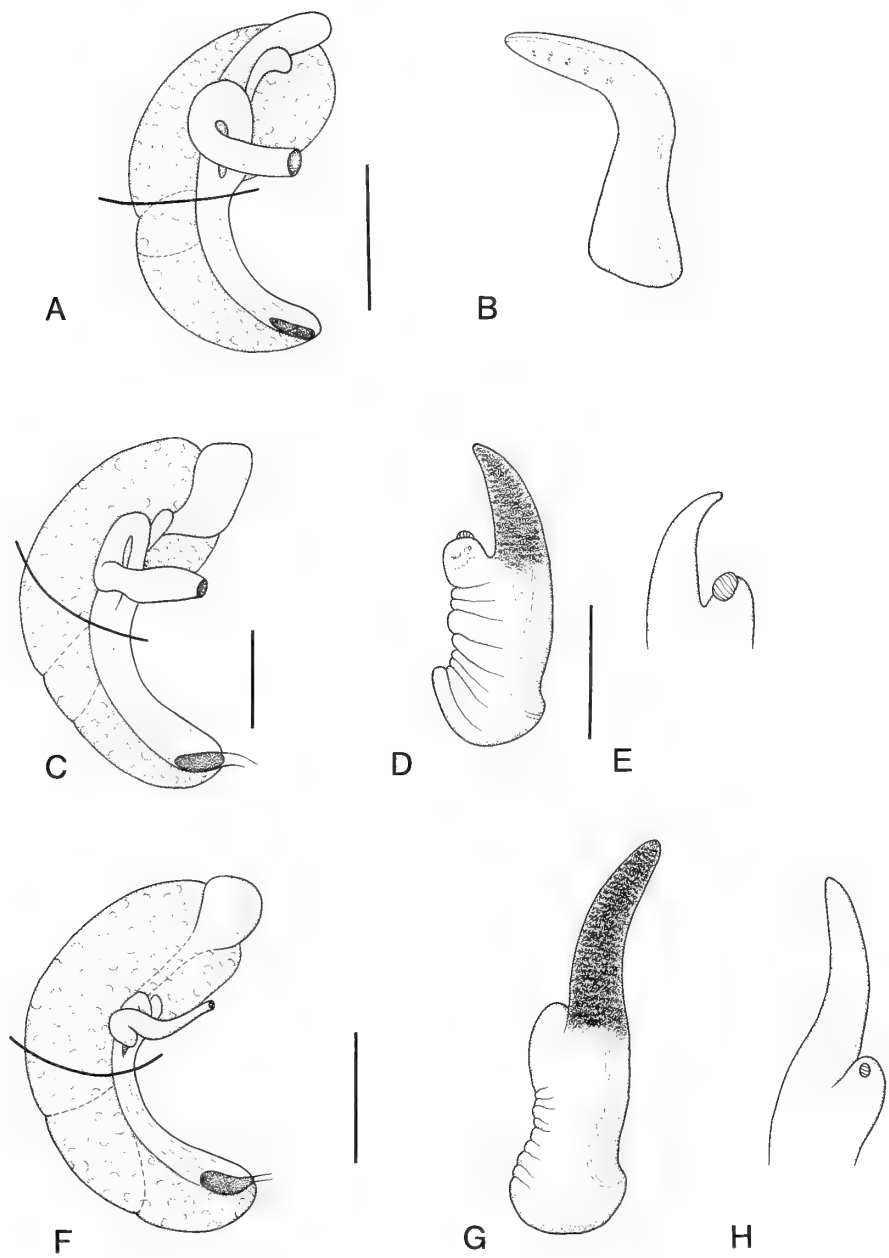


Figure 27

Genitalia of *Pyrgulopsis* species (A, B, *P. **coloradensis,*** USNM 873360, bar = 0.25 mm; C–E, *P. **montana,*** USNM 860694; F–H, *P. **hubbsi,*** USNM 873166). A. Female glandular oviduct and associated structures, bar = 0.25 mm. B. Dorsal aspect of penis, scale as in A. C. Female glandular oviduct and associated structures, bar = 0.25 mm. D. Dorsal aspect of penis, bar = 0.25 mm. E. Ventral aspect of distal penis, scale as in D. F. Female glandular oviduct and associated structures, bar = 0.5 mm. G. Dorsal aspect of penis, scale as in F. H. Ventral aspect of distal penis, scale as in G.

body pigmentation that those from White River Valley. The distribution of this snail is shown in Figure 50.

Material examined: NEVADA. *Nye County:* Hardy Springs, USNM 860711, USNM 873154, USNM 874373, USNM 874662.—Emigrant Springs (south), White River Valley (Figure 4B), T. 9 N, R. 62 E, NE ¼ section 30, USNM 874688.—Emigrant Springs (north), White River Valley, T. 9 N, R. 62 E, NE ¼ section 19, USNM 873170, USNM 883843.—Butterfield Springs, White River Valley, T. 7 N, R. 62 E, NE ¼ section 28, USNM 874378, USNM

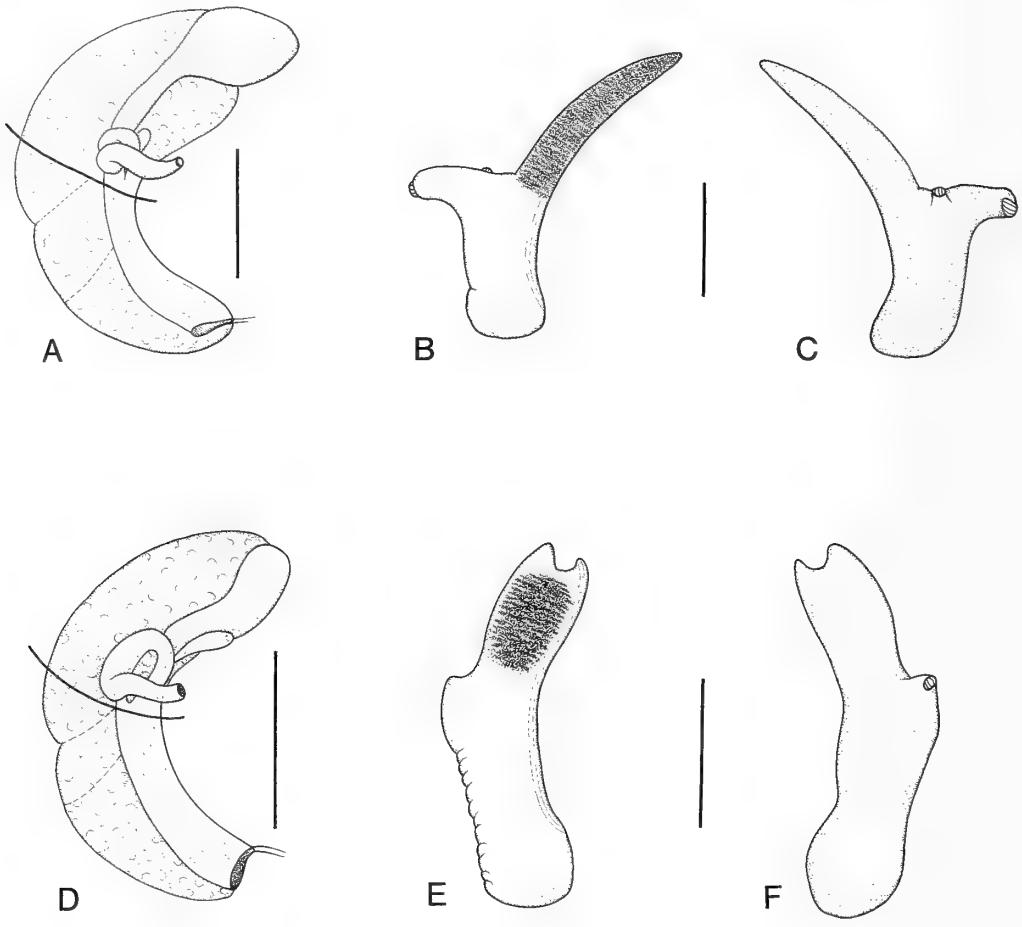


Figure 28

Genitalia of *Pyrgulopsis* species (A–C, *P.* ***sathos,*** USNM 860691; D–F, *P.* ***breviloba,*** USNM 860689). Bars = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of penis.

883972, USNM 883973. *Lincoln County:* Silver Springs, White River Valley, T. 8 N, R. 62 E, SW ¼ section 14, USNM 874672.—Springs, Parker Station, Cave Valley, T. 9 N, R. 64 E, NW ¼ section 6, USNM 874682. *White Pine County:* Ruppes Boghole, White River Valley, T. 10 N, R. 62 E, SE ¼ section 7, USNM 874685.

Species from Isolated Basins in Nevada

Pyrgulopsis ***turbatrix*** Hershler, sp. nov.

Southeast Nevada pyrg

(Figures 6K, 18G–J, 30D–F)

Pyrgulopsis micrococcus (Pilsbry, 1893), Hershler, 1989: 183 [not Pilsbry, 1893; in part; Frenchman Flat].—Hershler & Pratt, 1990:285, 286 [in part; northern Spring Mountains].

Etymology: *Turbatrix* (Latin), disturber, trouble-maker; referring to the difficulty encountered in separating this species from *P. micrococcus.*

Diagnosis: Medium-sized, with narrow-conic to turriform shell. Penis large; filament medium length, lobe medium length. Penial ornament a small terminal gland, and very small penial gland (sometimes absent).

Description: Shell (Figures 6K, 18G–J) narrow-conic to turriform, width/height, 56–76%; height, 2.1–3.6 mm; width, 1.5–2.2 mm; whorls, 4.25–5.5. Protoconch 1.4–1.5 whorls, diameter 0.36 mm; surface smooth except for very weak wrinkling at apex. Teleoconch whorls medium to highly convex, shoulders absent to well developed (often having weak sub-sutural angulation); body whorl often slightly disjunct behind the aperture. Aperture ovate, usually disjunct. Inner lip thin or slightly thickened, columellar shelf absent or narrow. Outer lip thin, orthocline or slightly prosocline,

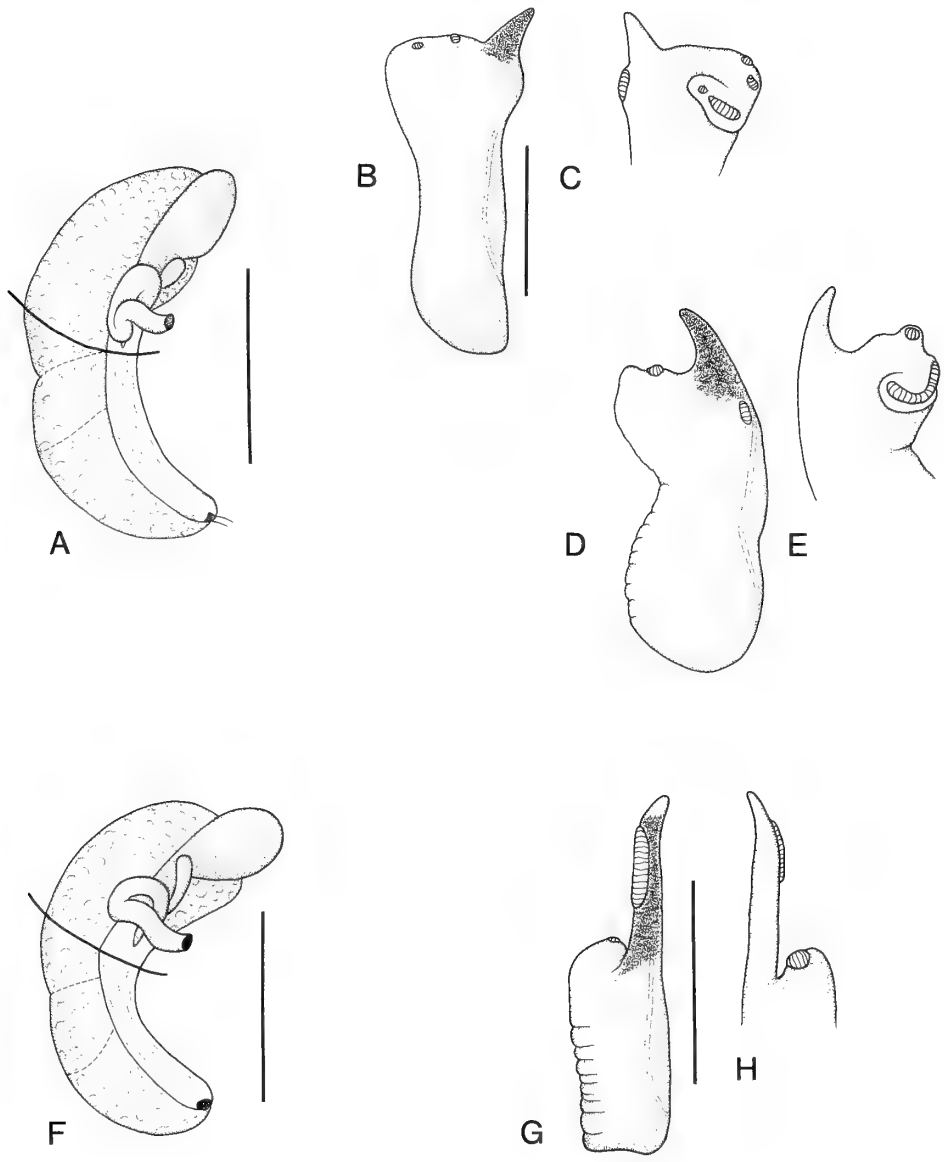


Figure 29

Genitalia of *Pyrgulopsis* species (A, D, E, *P.* ***lata,*** USNM 873167; B, C. *P.* ***lata,*** USNM 860697; F–H, *P.* ***gracilis,*** USNM 860698). A. Female glandular oviduct and associated structures, bar = 0.5 mm. B. Dorsal aspect of penis, bar = 0.5 mm. C. Ventral aspect of distal penis, scale as in B. D. Dorsal aspect of penis, scale as in B. E. Ventral aspect of distal penis, scale as in B. F. Female glandular oviduct and associated structures, bar = 0.5 mm. G. Dorsal aspect of penis, bar = 0.5 mm. H. Ventral aspect of distal penis, scale as in G.

without sinuation. Umbilicus rimate or shallowly perforate. Periostracum tan-brown.

Operculum ovate, amber, nuclear region slightly darker; nucleus eccentric; dorsal surface weakly frilled; outer margin having weak rim. Attachment scar slightly thickened all around.

Radula 650 × 100 μm, with 60 rows of teeth. Central tooth 25 μm wide, with medium to highly indented dorsal edge; lateral cusps, 5–6; central cusp narrow, daggerlike; basal cusps small. Basal process V-shaped, basal sockets medium depth. Lateral tooth formula 3(4)-1-4(5); neck medium flexed; outer wing 180% of cutting edge length. Inner marginal teeth with 19–22 cusps; cutting edge occupying 38% of length of tooth. Outer marginal teeth with 26–29 cusps; cutting edge occupying 30% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

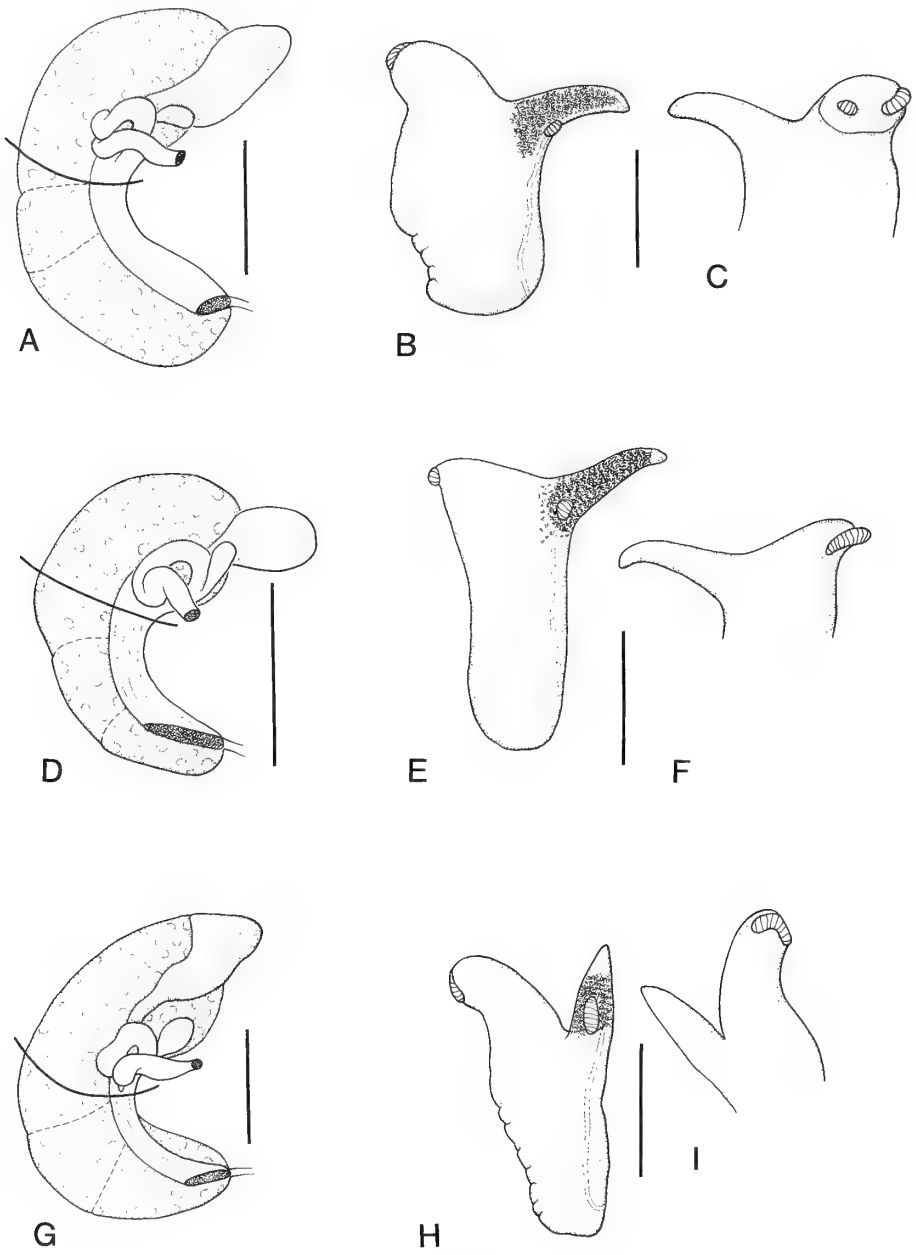


Figure 30

Genitalia of *Pyrgulopsis* species (A–C, *P.* ***marcida,*** USNM 874662; D–F, *P.* ***turbatrix,*** USNM 860699; G–I, *P.* ***sterilis,*** USNM 860714). Bars = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis.

Cephalic tentacles pigmented proximally with subepithelial medium grey streak; sometimes having light to medium grey epithelial cover as well. Snout, foot light to medium grey. Opercular lobe dark along inner edge. Neck unpigmented except for scattered black granules to medium grey. Pallial roof, visceral coil black. Penial filament darkly pigmented, distal base often similarly pigmented; remaining dorsal penis having scattered black pigment granules.

Ctenidial filaments, 18, pleated; ctenidium abutting or slightly overlapping pericardium posteriorly. Osphradium small (20–25%), narrowly ovate, positioned centrally or slightly posterior to middle of ctenidium. Renal gland longitudinal; kidney opening slightly thickened. Rectum

broadly overlapping pallial oviduct, slightly overlapping prostate gland.

Ovary 0.75–1.0 whorl, filling less than 50% of digestive gland behind stomach, slightly overlapping posterior stomach chamber. Distal female genitalia shown in Figure 30D. Albumen gland having medium pallial component. Capsule gland shorter, narrower than albumen gland, ovate in section; rectal furrow medium depth. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture an elongate, terminal slit having short anterior extension. Coiled oviduct a posterior-oblique loop (sometimes kinked at mid-length) usually preceded by a short posterior-oblique twist. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, ovate, longitudinal, usually positioned along ventral edge of gland, 50–67% of length posterior to gland. Bursal duct originating from anterior edge at mid-line, duct 50% of bursa length, medium width. Seminal receptacle medium-sized, pouchlike, positioned near ventral edge of albumen gland, overlapping anteriormost bursa.

Testis 2.0 whorls, filling more than 50% of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland bean-shaped (weakly curved), pallial portion short, ovate in section. Proximal pallial vas deferens straight, slightly undulating, or with weak bend. Penis (Figure 30E, F) large; base rectangular, weakly folded or smooth; filament medium length and width, tapering to point, oblique; lobe slightly shorter than filament, broadly triangular, slightly oblique. Terminal gland small, narrow (rarely ovate), usually longitudinal and ventral. Penial gland very small (often absent), considerably narrower than filament, positioned near base of filament. Penial duct straight, near outer edge.

Type locality: Horseshutem Springs, Pahrump Valley, Nye County, Nevada, T. 17 S, R. 53 E, SE ¼ section 27. Holotype, USNM 883978 (Figure 18G), collected by D. W. Sada, 20 July 1995; paratypes, USNM 860699. The type locality is a very small rheocrene highly impacted by cattle and water diversion (Figure 3A).

Remarks: This snail was previously confused with *P. micrococcus,* which also occurs in southeastern Nevada, but differs in its more elongate shell; narrower, usually longitudinal (not transverse) terminal gland on the penis; and frequent presence of a penial gland. *Pyrgulopsis* ***turbatrix*** also closely resembles *P.* ***sterilis*** (described below), which is found in isolated basins to the north, but differs in its broader penial lobe, smaller penial gland, and longitudinal orientation of terminal gland; and in having fewer cusps on the marginal radular teeth. *Pyrgulopsis* ***turbatrix*** occurs not only in several isolated basins in southwestern Nevada (Frenchman Flat, Indian Springs Valley, Pahrump Valley), but also in Colorado River drainage (Las Vegas Valley) and Death Valley system (Amargosa Flat) (Figure 50). Snails from Las Vegas Valley do not have a penial gland, but otherwise conform to *P.* ***turbatrix*** in all features.

Material examined: NEVADA. *Clark County:* La Madre Spring, Red Rock Wash, Las Vegas Valley, T. 20 S, R. 58 E, NW ¼ section 6, USNM 874458, USNM 883981.—Stream, east of Willow Spring, Red Rock Wash, Las Vegas Valley, T. 21 S, R. 58 E, NW ¼ section 4, USNM 874009, USNM 874020, USNM 874214, USNM 874455, USNM 883656.—Willow Spring, Red Rock Wash, Las Vegas Valley, T. 20 S, R. 58 E, SE ¼ section 32, USNM 873186.—Lost Canyon Spring, Red Rock Wash, Las Vegas Valley, T. 21 S, R. 58 E, NE ¼ section 4, USNM 883977.—Willow Spring, Indian Springs Valley, T. 18 S, R. 55 E, NE ¼ section 2, USNM 874765, USNM 883551.—Willow Creek (just below Willow Spring), Indian Springs Valley, T. 18 S, R. 55 E, section 2, USNM 854065.—Cold Creek Spring, Indian Springs Valley, T. 18 S, R. 55 E, SE ¼ section 1, USNM 854738, USNM 873451, USNM 883550. *Nye County:* Horseshutem Springs (Figure 3A), USNM 860699, USNM 883978.—Grapevine Springs, Amargosa Flat, T. 17 S, R. 53 E, SW ¼ section 21, USNM 874756, USNM 883980.—Cane Spring, Frenchman Flat, T. 13 S, R. 52 E, NE ¼ section 26, USNM 857936, USNM 874775.

Pyrgulopsis ***sterilis*** Hershler, sp. nov.

Sterile basin pyrg

(Figures 6L, 18K, L, 30G–I)

Etymology: *Sterilis* (Latin), unfruitful or barren; referring to occurrence of this species in the fishless region of south-central Nevada referred to as the "area of sterile basins" by Hubbs & Miller (1948).

Diagnosis: Medium-sized to large, with ovate- to narrow-conic shell. Penis medium-sized, filament and lobe medium length. Penial ornament of small terminal and penial glands.

Description: Shell (Figures 6L, 18K, L) ovate- to narrow-conic, apex often eroded; width/height, 63–83%; height, 2.2–4.0 mm; width, 1.8–2.6 mm; whorls, 3.75–5.25. Protoconch 1.3 whorls, diameter 0.38 mm, initial 0.75 whorl wrinkled, later portion smooth or having a few very weak spiral striae. Teleoconch whorls highly convex, sometimes weakly loosened, producing scalariform appearance, shoulders weakly developed. Aperture ovate, narrowly adnate or slightly disjunct. Inner lip thick in larger specimens, without columellar shelf. Outer lip thin, orthocline-weakly prosocline, without sinuation. Umbilicus rimate or shallowly perforate. Periostracum dark brown.

Operculum ovate, dark amber, nuclear region reddish; nucleus eccentric; dorsal surface weakly frilled. Attachment scar thick all around.

Radula 970 × 160 μm, with 69 rows of teeth. Central

tooth 31 μm wide, with medium indented dorsal edge; lateral cusps, 5–6; central cusp medium width, daggerlike or rounded; basal cusps small. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 3-1-3(4, 5); neck weakly flexed; outer wing 200% of cutting edge length. Inner marginal teeth with 26–29 cusps; cutting edge occupying 33% of length of tooth. Outer marginal teeth with 32–36 cusps; cutting edge occupying 25% of length of tooth. Stomach and style sac equal sized; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented, except for scattered internal, grey granules, to dark grey-black. Snout light to dark grey-black. Foot, neck light to medium grey. Opercular lobe usually dark along inner edge, sometimes also along sides or all around. Pallial roof, visceral coil uniform black. Penial filament darkly pigmented internally for most of length; pigment granules also sometimes scattered on base and lobe.

Ctenidial filaments, 22, strongly pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, centered posterior to middle of ctenidium. Renal gland longitudinal; kidney opening white, muscularized. Rectum broadly overlapping genital ducts.

Ovary 1.0–1.25 whorls, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber anteriorly. Distal female genitalia shown in Figure 30G. Albumen gland with short pallial component. Capsule gland shorter, but as wide as albumen gland, subcircular in section; rectal furrow well developed. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit, sometimes forming a weak papilla, having short anterior extension. Coiled oviduct a small, posterior-oblique loop, preceded and overlapped by similar loop or strong twist. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, ovate, often with abrupt narrowing near mid-line, longitudinal, with 50% of length posterior to gland. Bursal duct originating from anterior edge at mid-line, often poorly distinguished from bursa, 50% of bursa length, medium width, often shallowly embedded in albumen gland. Seminal receptacle small to medium-sized, pouchlike, overlapping or lateral (ventral side) to anterior portion of bursa.

Testis 2.0 whorls, filling more than 50% of digestive gland behind stomach, overlapping both stomach chambers anteriorly. Prostate gland bean-shaped, pallial portion short, ovate in section. Proximal pallial vas deferens having well-developed bend, sometimes slightly reflexed. Penis (Figure 30H, I) medium-sized; base rectangular, smooth or weakly folded; filament medium length and width, tapering to point, straight or slightly oblique; lobe knoblike, slightly longer than filament, slightly oblique. Terminal gland small, narrow, rarely divided into two units, curved, transverse, largely on ventral surface. Penial gland small, slightly narrower than filament, filling proximal half of filament and sometimes extending slightly onto base. Small, slightly raised, distal ventral gland seen in single specimen. Penial duct straight, near outer edge.

Type locality: Spring, Hunts Canyon Ranch, Ralston Valley, Nye County, Nevada, T. 8 N, R. 46 E, SW ¼ section 31 (Figure 50). Holotype, USNM 874876 (Figure 18K), collected by D. W. Sada, 8 November 1992; paratypes, USNM 860714. The type locality is a small rheocrene located in the middle of a pasture on a private ranch.

Remarks: This snail is contrasted with *P.* ***turbatrix*** above. Material collected from the type locality had a high incidence of trematode parasitism, which may be related to the occurrence of scalariform individuals in this sample.

Material examined: NEVADA. *Nye County:* Spring, Hunts Canyon Ranch, USNM 860714, USNM 874760, USNM 874876.—Spring, feeding pond at ranch house, Hunts Canyon Ranch, Ralston Valley, USNM 874767.—Sidehill Spring, (west) Stone Cabin Valley, T. 5 N, R. 47 E, SW ¼ section 26, USNM 874769, USNM 874877.

Pyrgulopsis ***ruinosa*** Hershler, sp. nov.

Fish Lake Valley pyrg

(Figures 7A, 18M, 31A–C)

Etymology: From *ruinosus* (Latin), going to ruin; referring to the current status of this species.

Diagnosis: Medium-sized, with ovate-conic shell. Penis large, filament and lobe short. Penial ornament a large terminal gland, small Dg1; large, fused Dg2–Dg3; and large ventral gland.

Description: Shell (Figures 7A, 18M) usually ovate-conic, rarely sub-globose or narrow conic; width/height, 63–80%; height, 2.6–3.3 mm; width, 1.8–2.3 mm; whorls, 4.25–5.0. Protoconch 1.3 whorls, diameter 0.44 mm; initial whorl finely wrinkled, later portion becoming smooth. Teleoconch whorls medium convexity, sutures deeply impressed; shoulders well developed; body whorl slightly disjunct behind the aperture in larger specimens. Aperture ovate, usually disjunct. Inner lip thin, without columellar shelf. Outer lip thin, orthocline or slightly prosocline, weakly sinuate. Umbilicus perforate. Periostracum tan.

Operculum ovate, amber, nuclear region darker; nucleus eccentric; dorsal surface weakly frilled; outer margin having weak rim. Attachment scar thick all around.

Radula 610 × 115 μm, with 60 rows of teeth. Central tooth 27 μm wide, with medium indented dorsal edge; lateral cusps, 5–7; central cusp broad, daggerlike; basal cusps small, sometimes accompanied by weak thickening on outside. Basal process often slightly shorter than lateral margins, V-shaped, basal sockets medium depth. Lateral tooth formula 2(3, 4)-1-3(4, 5); neck weakly flexed;

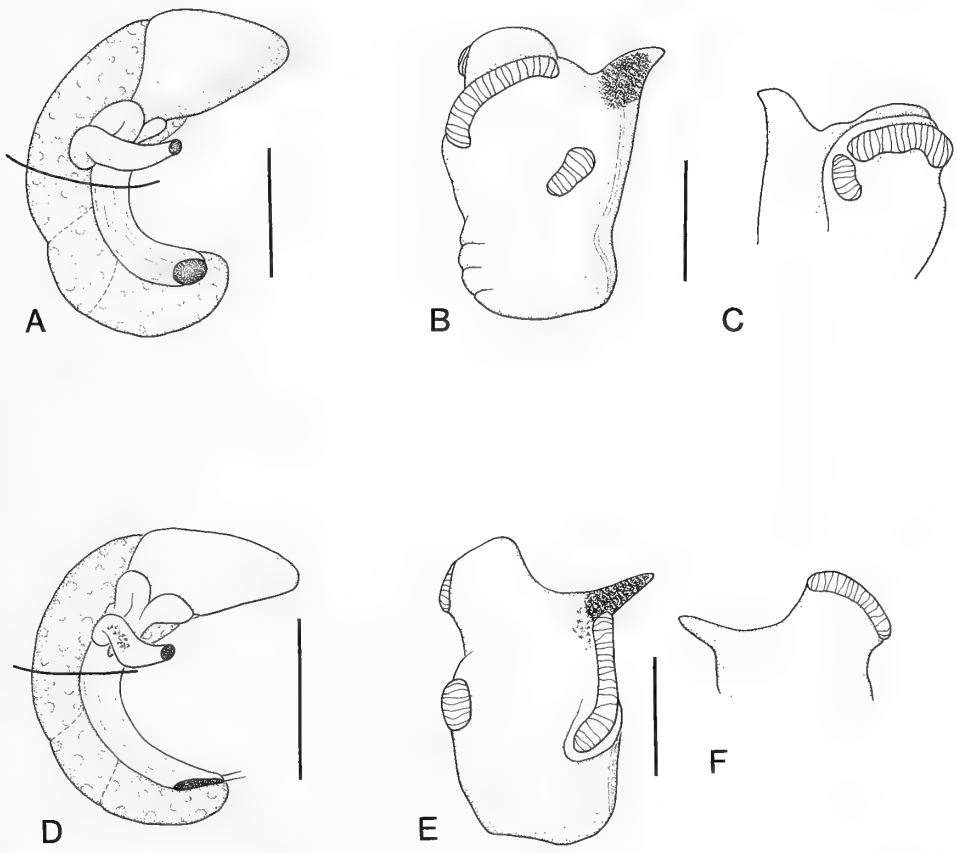


Figure 31

Genitalia of *Pyrgulopsis* species (A–C, *P. **ruinosa,*** USNM 860700; D–F, *P. **sublata,*** USNM 860724). Bars = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis.

outer wing 190% of cutting edge length. Inner marginal teeth with 20–28 cusps; cutting edge occupying 36% of length of tooth. Outer marginal teeth with 24–35 cusps; cutting edge occupying 28% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented or light grey-brown. Snout, foot unpigmented to dark grey-brown. Opercular lobe unpigmented or dark along inner edge, sometimes also darkly pigmented along sides. Neck unpigmented to medium grey-brown. Pallial roof, visceral coil light grey-brown to uniform black. Penial filament darkly pigmented internally.

Ctenidial filaments, 22, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, centered slightly posterior to middle of ctenidial axis. Renal gland longitudinal; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 1.0 whorl, filling 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 31A. Albumen gland having medium pallial component. Capsule gland shorter and as wide as albumen gland, sub-circular in section; rectal furrow absent to well developed. Ventral channel moderately overlapping capsule gland; longitudinal fold well developed. Genital aperture a sub-terminal pore; anterior extension absent or weakly developed. Coiled oviduct a posterior-oblique loop preceded by prominent posterior twist or small coil. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix 50% as long as albumen gland, as wide as gland, broadly ovate to pyriform, longitudinal, with most of length posterior to gland. Bursal duct originating from anterior edge near mid-line, medium length and width. Seminal receptacle small, pouchlike, overlapping anteriormost bursa, often positioned near ventral edge of albumen gland.

Testis 1.5 whorls, filling almost all of digestive gland behind stomach, overlapping posterior and part of anterior stomach chamber. Prostate gland large, elongate bean-shaped, pallial portion medium, ovate in section. Proximal pallial vas deferens having well-developed,

reflexed loop. Penis (Figure 31B, C) large; base rectangular, often folded along inner edge; filament short, medium width, tapering to point, slightly oblique; lobe short, squarish, broad, slightly oblique. Terminal gland large, narrow, curving, transverse, largely on ventral surface. Dg1 small, rarely dotlike, absent, or fragmented into two units, usually longitudinal, medial or positioned slightly proximal to filament. Dg2 and Dg3 usually fused into single, large, curved unit (rarely fused with Dg1) transversely positioned near distal edge of lobe; gland sometimes accompanied by one to two small units positioned alongside (sometimes abutting or fused to) proximal edge. Ventral gland large, rarely absent or accompanied by second, dotlike unit; borne on prominent swelling, longitudinal-transverse, positioned near base of lobe. Penial duct straight, near outer edge.

Type locality: Spring, southwest of The Crossing, Fish Lake Valley, Esmeralda County, Nevada, T. 1 N, R. 36 E, SW ¼ section 16 (Figure 50). Holotype, USNM 873407 (Figure 18M), collected by R. Hershler and D. Giuliani, 16 July 1988; paratypes, USNM 860700. The type locality, a small, thermal (26°C.) limnocrene, is the northernmost of a series of five springs on a large ranch (Figure 4C). Snails were collected in the shallow outflow, and were absent both in the spring pool and in other springs of this complex. This species has not been collected on subsequent visits to this now degraded area and is probably extinct.

Remarks: Although not closely similar to any congener, this species resembles *P. gibba* and a group of species found in the Owens Valley region in that its penis is relatively well ornamented with glands, but lacks a penial gland. *Pyrgulopsis* ***ruinosa*** differs from the above species in having a relatively large Dg1, long, fused Dg2–3, and short penial filament.

Material examined: NEVADA. *Esmeralda County:* Spring, southwest of The Crossing (Figure 4C), USNM 860700, USNM 873407.

Pyrgulopsis ***sublata*** Hershler, sp. nov.

Lake Valley pyrg

(Figures 7B, 12E, 18N, O, 31D–F)

Etymology: From *sublatus* (Latin), raised aloft; referring to the prominently raised or frilled opercular whorls characterizing this species.

Diagnosis: Medium-sized, with broadly to ovate-conic shell. Penis large, filament and lobe short. Penial ornament a large terminal gland, large Dg1, and small Dg2.

Description: Shell (Figures 7B, 18N, O) broadly to ovate-conic, width/height, 66–78%; height, 2.2–2.7 mm; width, 1.4–2.0 mm; whorls, 4.5–5.0. Protoconch 1.4 whorls, diameter 0.35 mm; surface smooth except for very weak wrinkling around apex and faint spiral striae on later portion. Teleoconch whorls medium to highly convex, shoulders weak or absent; sculpture including occasional faint spiral striae. Aperture ovate, adnate or slightly disjunct. Inner lip usually thin; columellar shelf very narrow or absent. Outer lip usually thin, orthocline or weakly prosocline, weakly sinuate. Umbilicus rimate or shallowly perforate. Periostracum tan.

Operculum (Figure 12E) ovate, multispiral, amber, nuclear region reddish; nucleus eccentric; dorsal surface strongly frilled; outer margin having weak rim. Attachment scar thick along most of perimeter, broadly so between nucleus and inner edge; whorl outlines strongly bulging.

Radula 645 × 100 μm, with 63 rows of teeth. Central tooth 22 μm wide, with highly indented dorsal edge; lateral cusps, 7–9; central cusp rounded; basal cusps medium-sized, sometimes accompanied by weak thickening to outside. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 4(5)-1-5(6); neck weakly flexed; outer wing 215% of cutting edge length. Inner marginal teeth with 26–32 cusps; cutting edge occupying 29% of length of tooth. Outer marginal teeth with 27–34 cusps; cutting edge occupying 27% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented to medium grey. Snout, foot light to medium grey. Opercular lobe having black smear all around. Neck unpigmented to medium grey. Pallial roof, visceral coil medium grey-brown to black, pigment not uniform. Penial filament and adjacent portion of base darkly pigmented.

Ctenidial filaments, 17, pleated; pericardium overlapping ctenidium posteriorly. Osphradium small, narrow, centered well posterior to middle of ctenidium. Renal gland longitudinal; kidney opening slightly thickened. Rectum broadly overlapping genital ducts.

Ovary 0.5 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 31D. Albumen gland with medium-large (30–40%) pallial component. Capsule gland shorter, narrower than albumen gland, ovate in section; rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct of two slightly or greatly overlapping posterior-oblique loops; proximal loop often weakly developed, usually having weak pigment streak on proximal arm. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copulatrix 67% as long and often as wide as albumen gland, elongate-pyriform, longitudinal, with most of length posterior to gland. Bursal duct originating from anterior edge at midline, medium length, medium width. Seminal receptacle small, pouchlike, overlapping anteriormost bursa, extending to edge of albumen gland.

Testis 1.5 whorls, filling more than 50% of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland large, bean-shaped, pallial portion medium, ovate in section. Proximal pallial vas deferens having well-developed, reflexed loop. Penis (Figure 31E, F) large, broadly rectangular, weakly folded or smooth; filament short, narrow, tapering to point, oblique; lobe short (usually as long as filament), square (rarely club-like), slightly oblique. Terminal gland large, narrow, rarely ovate or bifurcate; transverse, largely ventral. Dg1 extending from base of filament (sometimes slightly overlapping filament) along outer edge to medial position and then curving inward a short distance; proximal portion borne on low swelling; gland occasionally split into two similarly sized, abutting units. Dg2 small, ovate, medial (or slightly basal to middle of penis), borne along inner edge (often protruding slightly), usually longitudinal or slightly oblique, sometimes curving transversely toward Dg1. Penial duct straight, near outer edge.

Type locality: Wambolt Springs, Lake Valley, Lincoln County, Nevada, T. 9 N, R. 65 E, NE ¼ section 23 (Figure 50). Holotype, USNM 874681 (Figure 18N), collected by R. Hershler and P. Hovingh, 26 June 1992; paratypes, USNM 860724. The type locality is a shallow, but broad (8 m) helocrene, slightly disturbed by livestock.

Remarks: Among the group of species whose penes have an elongate Dg1, *P.* ***sublata*** resembles several species from Verde River drainage (see Hershler & Landye, 1988) and some populations herein referred to *P. kolobensis* in also having a well-developed Dg2 along the inner edge of the penis. *Pyrgulopsis* ***sublata*** differs from these species in lacking a ventral gland on the penis and in having a very strongly frilled, multispiral operculum.

Material examined: NEVADA. *Lincoln County:* Wambolt Springs, Lake Valley, T. 9 N, R. 65 E, NE ¼ section 23, USNM 860724, USNM 874681.

Pyrgulopsis ***lockensis*** Hershler, sp. nov.

Lockes pyrg

(Figures 7C, 12F, 14G–I, 19A, 32A–C)

Etymology: Referring to endemism of this species at Lockes, Duckwater Valley.

Diagnosis: Small, with sub-globose to ovate-conic shell. Penis large, filament very short, lobe absent. Penial ornament absent.

Description: Shell (Figures 7C, 19A) sub-globose to ovate-conic, width/height, 80–93%; height, 1.6–1.9 mm; width, 1.4–1.6 mm; whorls, 3.25–4.5. Protoconch 1.2 whorls, diameter 0.29 mm, weakly wrinkled along inner edge near apex, later portion smooth, with a few weak spiral striations. Teleoconch whorls highly convex; shoulders narrow or absent. Aperture sub-circular, usually adnate, rarely disjunct. Inner lip medium thickness, without columellar shelf. Outer lip thin, orthocline or slightly prosocline, weakly sinuate. Umbilicus perforate. Periostracum tan.

Operculum (Figure 12F) broadly ovate, light amber; nucleus slightly eccentric; dorsal surface frilled. Attachment scar thick all around.

Radula (Figure 14G–I) 570 × 90 μm, with 47 rows of teeth. Central tooth 20 μm wide, with medium indented dorsal edge; lateral cusps, 5–6; central cusp narrow, daggerlike; basal cusps medium-sized. Basal process U-shaped, basal sockets medium depth. Lateral tooth formula 3-1-3(4); neck weakly flexed; outer wing 190% of cutting edge length. Inner marginal teeth with 21–24 cusps, including large near basal cusp offset from others; cutting edge occupying 46% of length of tooth. Outer marginal teeth with 25–31 cusps; cutting edge occupying 29% of length of tooth. Stomach slightly longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum very small.

Cephalic tentacles, snout unpigmented or light grey-brown. Foot unpigmented or light grey-brown, darker along anterior edge. Opercular lobe black along inner edge. Neck unpigmented except for internal grey granules. Pallial roof, visceral coil usually light-medium grey-brown, rarely black, pigment usually darker on anterior mantle. Penis unpigmented.

Ctenidial filaments, 20, pleated; ctenidium overlapping pericardium posteriorly. Osphradium medium-sized, narrow, centered slightly posterior to middle of ctenidium. Renal gland oblique; kidney opening white. Rectum broadly overlapping genital ducts.

Ovary a little less than 1.0 whorl, filling more than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 32A. Albumen gland having very short pallial component. Capsule gland slightly shorter and narrower than albumen gland, sub-circular in section; rectal furrow weakly developed. Ventral channel overlapping capsule gland to medium extent; longitudinal fold well developed. Genital aperture a short slit opening near middle of capsule gland; anterior extension short. Coiled oviduct a tight, circular loop kinked proximally or at mid-length. Oviduct and bursal duct joining just behind pallial wall. Bursa copulatrix medium length and width, narrowly-ovate, often curved, usually oblique, with 33% of length posterior to albumen gland, anterior edge often shallowly embedded in gland. Bursal duct originating from or near anterior edge at mid-line, short, medium width. Seminal receptacle very small, pouchlike, overlapping anteriormost portion of bursa, often shallowly embedded in albumen gland.

Testis 1.0 whorl, filling 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Prostate gland bean-shaped, pallial portion short, narrowly ovate in section. Proximal pallial vas deferens straight. Penis (Figure 32B, C) large; base elongate, smooth, sometimes having sub-terminal bulge; filament very

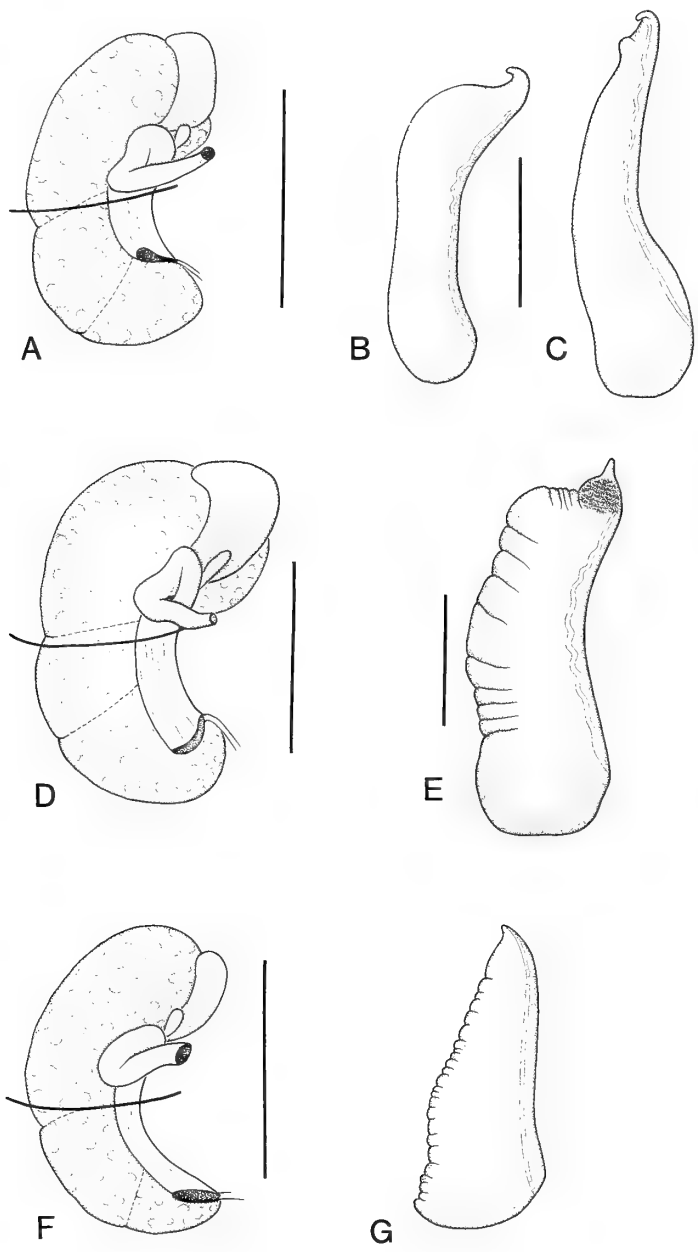


Figure 32

Genitalia of *Pyrgulopsis* species (A–C, *P.* ***lockensis,*** USNM 874879; D, E, *P.* ***papillata,*** USNM 860678; F, G, *P.* ***carinata,*** USNM 860680). Bars = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis.

short, narrow, usually tapering to point, longitudinal or slightly oblique, usually curved; lobe and glands absent. Penial duct weakly undulating distally, near outer edge.

Type locality: Spring, Lockes, Duckwater Valley, Nye County, Nevada, T. 8 N, R. 56 E, NE ¼ section 15 (Figure 50). Holotype, USNM 874779 (Figure 19A), collected by D.W. Sada, 5 October 1992; paratypes, USNM 860679. The type locality is a large, thermal (30°C.) limnocrene.

Remarks: This snail, and two other species endemic to Duckwater Valley (*P.* ***papillata,*** *P.* ***carinata***; described next), the northern extension of Railroad Valley, are united by small size, broadly conical shell with thin inner lip,

pale body pigmentation, simply coiled female oviduct, very small seminal receptacle; and simple, bladelike penis having very short filament; and probably compose a local radiation. This species is closely similar to *P. **papillata*** (which occurs a short distance to the north), as the snails share additional distinctive features of low trochoid or sub-globose shell, prominent spiral striae on the late protoconch, weakly undulating or straight pallial vas deferens, undulating penial duct, and sub-terminal or medial opening to the female genital duct. *Pyrgulopsis **lockensis*** differs from *P. **papillata*** in its weaker protoconch sculpture, smaller bursa copulatrix; and narrower penis, with less prominent filament lacking a distinct terminal papilla.

Material examined: NEVADA. *Nye County:* Spring, Lockes, USNM 860679, USNM 873168, USNM 874017, USNM 874779, USNM 874879.

*Pyrgulopsis **papillata*** Hershler, sp. nov.

Big Warm Spring pyrg

(Figures 7D, 11E, 19B, 32D, E)

Etymology: From *papillatus* (Latin), papillate, referring to the prominent terminal papilla on the penis of this species.

Diagnosis: Small, with sub-globose shell. Penis large, filament very short, lobe absent. Penial ornament absent.

Description: Shell (Figures 7D, 19B) sub-globose; width/height, 80–92%; height, 1.8–2.2 mm; width, 1.6–1.9 mm; whorls, 3.25–3.75. Protoconch (Figure 11E) 1.2 whorls, diameter 0.29 mm, initial 0.75 whorl sculptured with irregular, coarse wrinkles, sculpture coalescing in later portion to form a few, widely spaced spiral elements. Teleoconch whorls medium to highly convex, shoulders weakly developed or absent. Aperture broadly ovate, adnate or slightly disjunct. Inner lip slightly thickened, without columellar shelf. Outer lip thin, orthocline or slightly prosocline, weakly sinuate. Umbilicus perforate. Periostracum light tan.

Operculum ovate, light amber; nucleus slightly eccentric; dorsal surface frilled. Attachment scar thick almost all around, especially so between nucleus and inner edge and along inner edge.

Radula 535 × 86 μm, with 57 rows of teeth. Central tooth 20 μm wide, with medium indented dorsal edge; lateral cusps, 6–7; central cusp narrow, daggerlike, basal cusps small. Basal process broad, almost U-shaped, basal sockets medium depth. Lateral tooth formula 3(4, 5)-1-4(5); neck weakly flexed; outer wing 200% of cutting edge length. Inner marginal teeth with 24–28 cusps; cutting edge occupying 35% of length of tooth. Outer marginal teeth with 25–29 cusps; cutting edge occupying 24% of length of tooth. Stomach longer than style sac; anterior stomach chamber larger and posterior chamber; stomach caecum very small or absent.

Animal generally very pale. Cephalic tentacles, snout, neck, foot usually unpigmented, rarely light to medium brown. Opercular lobe often having distinctive black streak along inner edge. Pallial roof, visceral coil light to medium brown or red; testis often black. Penial filament darkly pigmented internally.

Ctenidial filaments, 30, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, positioned alongside posterior half of ctenidium. Renal gland longitudinal; kidney opening grey. Rectum broadly overlapping genital ducts.

Ovary 1.0 whorl, filling 50% of digestive gland behind stomach, slightly overlapping posterior stomach chamber. Distal female genitalia shown in Figure 32D. Albumen gland without pallial component. Capsule gland as long as, but slightly narrower than albumen gland, sub-circular in section, with short component behind pallial wall; rectal furrow weakly developed. Ventral channel narrowly overlapping capsule gland; longitudinal fold well developed. Genital aperture a sub-terminal slit having short anterior extension. Coiled oviduct a tight circular loop, usually kinked proximally or in mid-section. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copulatrix short, narrow, pyriform, oblique-transverse, pressed against edge of albumen gland with 33% of length posterior to gland. Bursal duct originating at or near anterior edge at mid-line, short, medium width, slightly embedded in albumen gland along ventral edge. Seminal receptacle very small, narrow, overlapping anterior bursa near ventral edge.

Testis 1.25 whorls, filling most of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland ovate, pallial portion short, ovate in section. Proximal pallial vas deferens having weak bend or series of undulations. Penis (Figure 32E) large; base rectangular-elongate, often distally swollen, folded along inner edge; filament very short, medium width, bulbous, sub-longitudinal, terminating in narrow papilla; lobe absent or a very short bulge; glands absent. Penial duct near outer edge, undulating.

Type locality: Big Warm Spring, Duckwater Valley, Nye County, Nevada, T. 13 N, R. 56 E, SE ¼ section 32. Holotype, USNM 873185 (Figure 19B), collected by J.J. Landye, 3 September 1973; paratypes, USNM 860678. The type locality is a large, thermal (31°C.) limnocrene (Figure 4D), which flows into a canal system, located on the Duckwater Indian Reservation. Snails were collected from aquatic vegetation (Bladderwort) in the spring pool.

Remarks: This species is compared to *P. **lockensis*** above. The distribution of this snail is shown in Figure 50.

Material examined: NEVADA. *Nye County:* Big Warm Spring (Figure 4D), USNM 860678, USNM 873185, USNM 874772.—Little Warm Spring, Duckwater Valley,

T. 12 N, R. 56 E, NE ¼ section 5, USNM 883974, USNM 892016.

Pyrgulopsis ***carinata*** Hershler, sp. nov.

Carinate Duckwater pyrg

(Figures 7E, 19C, 32F, G)

Etymology: From *carinatus* (Latin), keeled; referring to the prominently carinate late teleoconch whorls on shells of this species.

Diagnosis: Medium-sized, with ovate-conic, distinctly carinate shell. Penis medium-sized; filament very short, lobe absent. Penial ornament absent.

Description: Shell (Figures 7E, 19C) ovate-conic, width/height, 78–89%; height, 1.8–2.5 mm; width, 1.6–2.0 mm; whorls, 3.5–4.0. Protoconch 1.1 whorls, diameter 0.28 mm, earliest portion finely wrinkled, otherwise smooth. Teleoconch whorls flat or slightly convex, shoulders broad, forming strong carina on final 2.5 whorls. Aperture ovate, adnate or slightly disjunct. Inner lip thick, without columellar shelf. Outer lip thin, orthocline, without sinuation. Umbilicus perforate to broadly open. Periostracum light tan.

Operculum ovate, amber; nucleus eccentric; dorsal surface weakly frilled; outer margin having rim. Attachment scar thick all around.

Radula 590 × 85 μm, with 62 rows of teeth. Central tooth 24 μm wide, with medium indented dorsal edge; lateral cusps, 5–6; central cusp medium width, dagger-like; basal cusps small. Basal tongue broad V- or U-shaped, basal sockets medium depth. Lateral tooth formula 3(4)-1-4(5); neck weakly flexed; outer wing 200% of cutting edge length. Inner marginal teeth with 24–28 cusps; cutting edge occupying 39% of length of tooth. Outer marginal teeth with 23–31 cusps; cutting edge occupying 28% of length of tooth. Stomach slightly longer than style sac; anterior stomach chamber slightly larger than posterior chamber; stomach caecum absent or very small.

Cephalic tentacles unpigmented or with medium brown stripe near bases. Snout, foot unpigmented. Opercular lobe often having black streak along inner edge and sides, otherwise unpigmented. Neck unpigmented or with scattered internal grey granules. Pallial roof, visceral coil unpigmented to medium brown-black; pigment usually lighter on pallial roof. Penial filament sometimes darkly pigmented internally.

Ctenidial filaments, 23, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, positioned alongside posterior half of ctenidium. Renal gland longitudinal; kidney opening grey. Rectum broadly overlapping pallial oviduct, slightly overlapping prostate gland.

Ovary 0.5–0.75 whorl, filling more than 50% of digestive gland behind stomach, abutting edge of stomach anteriorly. Distal female genitalia shown in Figure 32F. Albumen gland with very short or no pallial component. Capsule gland shorter and narrower than albumen gland, ovate in section; rectal furrow absent. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit with short anterior extension. Coiled oviduct a tight, circular loop. Oviduct and bursal duct joining just behind pallial wall. Bursa copulatrix short, narrow, narrowly ovate-tubular, longitudinal, extending to posterior edge of albumen gland; positioned along ventral edge of gland, with portion (rarely entirety) extending onto right side. Bursal duct originating from anterior edge at mid-line, often poorly distinguished from bursa, shorter than bursa, medium width. Seminal receptacle very small, pouchlike, overlapping anteriormost bursa of proximal bursal duct.

Testis 1.0 whorl, filling more than 50% of digestive gland behind stomach, partly overlapping posterior stomach chamber. Prostate gland bean-shaped, entirely visceral or with very short pallial portion, ovate in section. Proximal pallial vas deferens straight or with very small bend. Penis (Figure 32G) medium-sized; base rectangular, usually folded along inner edge, slightly narrowed proximally, distally tapering; filament weakly distinguished from base, very short, medium width, strongly tapered, terminating in narrow, pointed papilla, longitudinal; lobe and glands absent. Penial duct straight, near outer edge.

Type locality: Little Warm Spring, Duckwater Valley, Nye County, Nevada, T. 12 N, R. 56 E, NE ¼ section 5 (Figure 51). Holotype, USNM 883975 (Figure 19C), collected by J.J. Landye, 3 September 1973; paratypes, USNM 860680. The type locality is a large, thermal (30°C.) limnocrene on the Duckwater Indian Reservation.

Remarks: As mentioned above, this species shares unusual features with *P.* ***papillata*** (with which it co-occurred in Little Warm Spring) and *P.* ***lockensis.*** *Pyrgulopsis* ***carinata*** differs from the above in its strongly carinate shell, smoother protoconch (lacking any spiral striae), simply tapering penis, and more distal capsule gland opening. This snail was collected from the type locality in 1973. During two recent visits to this spring the species could not be found (although *P.* ***papillata*** still is present), and it is likely extinct.

Material examined: NEVADA. *Nye County:* Little Warm Spring, USNM 860680, USNM 883975.

Pyrgulopsis ***aloba*** Hershler, sp. nov.

Duckwater pyrg

(Figures 7F, 19D, E, 33A, B)

Etymology: From *lobus* (Latin), projection; referring to absence of a lobe on the penis of this species.

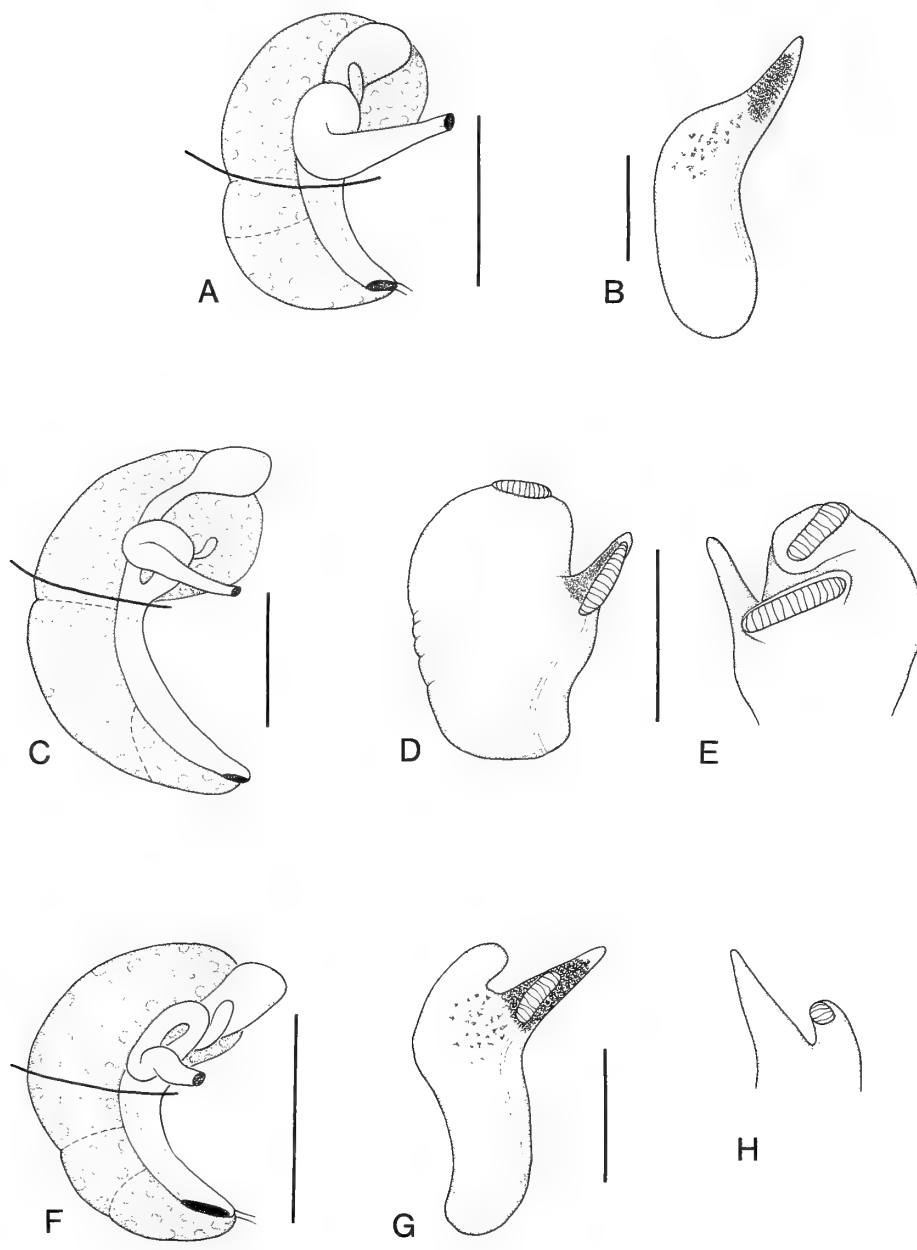


Figure 33

Genitalia of *Pyrgulopsis* species (A, B, *P.* ***aloba,*** USNM 860681; C–E, *P.* ***villacampae,*** USNM 860712; F–H, *P.* ***anatina,*** USNM 860710). A. Bar = 0.25 mm. B. Bar = 0.25 mm. C–H. Bars = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis (not shown for *P.* ***aloba*** as penial ornament absent).

Diagnosis: Small, with sub-globose to ovate-conic shell. Penis medium-sized; filament medium length, lobe absent. Penial ornament absent.

Description: Shell (Figures 7F, 19D, E) sub-globose to ovate-conic, apex usually eroded, width/height, 80–96%; height, 1.0–1.9 mm; width, 1.0–1.7 mm; whorls, 2.5–4.0. Protoconch 1.25 whorls, diameter 0.25 mm, finely wrinkled, but becoming near smooth near teleoconch border. Teleoconch whorls moderately convex, shoulders weak, but sometimes forming pronounced sub-sutural angulation on body whorl. Aperture ovate, angled above, usually adnate. Inner lip thick, sometimes forming narrow

columellar shelf. Outer lip thin, prosocline, without sinuation. Umbilicus absent-rimate. Periostracum light brown-tan.

Operculum ovate, amber, reddish in nuclear region; nucleus eccentric; dorsal surface frilled. Attachment scar sometimes thick along inner edge.

Radula 418 × 63 μm, with 62 rows of teeth. Central tooth 14 μm wide, with medium indented dorsal edge; lateral cusps, 5–7; central cusp medium width, dagger-like; basal cusps medium-sized. Basal tongue broad V-shaped, basal sockets medium depth. Lateral tooth formula 3-1-5(6); neck weakly flexed; outer wing 220% of cutting edge length. Inner marginal teeth with 23–26 cusps; cutting edge occupying 33% of length of tooth. Outer marginal teeth with 27–29 cusps; cutting edge occupying 26% of length of tooth. Stomach slightly longer than style sac; stomach chambers equal-sized; stomach caecum very small or absent.

Cephalic tentacles light to medium grey-brown; pigment often concentrated as short longitudinal strip proximally. Snout light to dark grey-brown. Foot light to medium grey. Inner edge of opercular lobe black. Neck unpigmented to medium grey. Pallial roof, visceral coil dark brown-black. Penial filament darkly pigmented internally, distal portion of base having scattered black granules.

Ctenidial filaments, 11, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, ovate, positioned centrally or slightly posterior to middle of ctenidium. Renal gland oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.5 whorl, filling 50% or slightly more of digestive gland behind stomach, overlapping posterior stomach chamber anteriorly. Distal female genitalia shown in Figure 33A. Albumen gland without pallial component. Capsule gland slightly shorter and narrower than albumen gland, ovate in section; rectal furrow deep. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a single, tight circular loop. Oviduct and bursal duct joining slightly behind pallial wall. Oviduct opening to albumen gland at pallial wall. Bursa copulatrix short, narrow, narrowly ovate, longitudinal, extending to or just proximal to edge of gland. Bursal duct originating from anterior edge at mid-line, close to oviduct, slightly shorter than bursa, medium width. Seminal receptacle small, pouch-like, overlapping anterior portion of bursa.

Testis 0.75 whorl, filling more than 50% of digestive gland behind stomach, overlapping posterior stomach chamber anteriorly. Prostate gland bean-shaped, pallial portion very short; narrowly ovate in section. Proximal pallial vas deferens having small bend. Penis (Figure 33B) medium-sized; base rectangular, lacking folds; filament medium length and width, tapering to point, slightly oblique; lobe and glands absent. Penial duct very close to outer edge, straight.

Type locality: Spring, northwest of Duckwater, Duckwater Valley, Nye County, Nevada, T. 13 N, R. 56 E, center section 31. Holotype, USNM 883847 (Figure 19D), collected by R. Hershler and P. Hovingh, 12 July 1994; paratypes, USNM 860681. The type locality is a small rheocrene on the Duckwater Indian Reservation.

Remarks: This species resembles some of the other locally endemic forms from Duckwater Valley (especially *P. **carinata***) in having a simple penis, but differs in having much stronger body pigment, larger oviduct coil, more anteriorly positioned bursa copulatrix, and smooth penis with larger filament. Snails collected at the head of a small spring (USNM 873187) about 2.0 km southeast of the type locality closely conform to *P. **aloba*** in all respects, while the outflow of this same spring yielded much larger, taller snails (USNM 873189) having highly stunted penes that otherwise conformed to those of this species. Additional collections will have to be made to better evaluate this interesting dimorphism. The distribution of this species is shown in Figure 51.

Material examined: NEVADA. *Nye County:* Spring, northwest of Duckwater, USNM 860681, USNM 883847.—Spring (source), east-southeast of Duckwater, Duckwater Valley, T. 12 N. R. 56 E, SW ¼ section 5, USNM 873187.—Spring (outflow), east-southeast of Duckwater, Duckwater Valley, T. 12 N, R. 56 E, SW ¼ section 5, USNM 873189.

*Pyrgulopsis **villacampae,*** Hershler, sp. nov.

Duckwater Warm Springs pyrg

(Figures 7G, 13A, 19F, G, 33C–E)

Etymology: Named after Yolanda Villacampa, who assisted with much of the laboratory work associated with this project.

Diagnosis: Medium-sized, with trochiform-neritiform shell. Penis large, filament and lobe medium length. Penial ornament a medium-sized terminal gland, large penial gland, and large ventral gland.

Description: Shell (Figures 7G, 19F, G) trochiform-neritiform, apex often eroded, width/height, 81–94%; height, 2.5–3.7 mm; width, 2.3–3.1 mm; whorls, 3.5–4.5. Protoconch 1.2 whorls, diameter 0.33 mm; initial 0.75 whorl sculptured with widely separated, raised wrinklelike elements, later portion smooth. Teleoconch whorls medium-highly convex, sometimes having weak sub-sutural angulation on body whorl. Aperture broadly ovate, usually adnate. Inner lip thin, without columellar shelf. Outer lip thin, prosocline, strongly sinuate. Umbilicus rimate-narrow. Periostracum tan.

Operculum (Figure 13A) broadly ovate, light amber; nucleus sub-central; dorsal surface frilled; outer margin

having weak rim. Attachment scar slightly thickened between nucelus and inner edge.

Radula 1.09 mm × 130 μm, with 63 rows of teeth. Central tooth 33 μm wide, with highly indented dorsal edge; lateral cusps, 4–6; central cusp narrow, daggerlike; basal cusps small. Basal process V-shaped, basal sockets medium depth. Lateral tooth formula 3(4)-1-4(5); neck weakly flexed; outer wing 130% of cutting edge length. Inner marginal teeth with 23–26 cusps; cutting edge occupying 38% of length of tooth. Outer marginal teeth with 27–29 cusps; cutting edge occupying 24% of length of tooth. Stomach as long or slightly shorter than style sac; anterior chamber slightly larger; stomach caecum very small.

Cephalic tentacles unpigmented to medium brown. Snout unpigmented to dark brown-black. Foot unpigmented to medium brown, sole often grey. Opercular lobe unpigmented or brown along sides. Neck unpigmented to light brown. Pallial roof, visceral coil light to dark brown, red, or black, often uniformly pigmented. Penial filament darkly pigmented internally.

Ctenidium very wide; filaments, 43, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, positioned alongside posterior half of ctenidium. Renal gland oblique; kidney opening grey. Rectum broadly overlapping pallial oviduct, scarcely or not overlapping prostate gland.

Ovary 1.0–1.25 whorls, filling almost all of digestive gland behind stomach, overlapping posterior and part of anterior stomach chambers. Distal female genitalia shown in Figure 33C. Albumen gland having short or no pallial component. Capsule gland longer (sometimes markedly so), but narrower than albumen gland, anterior section markedly distal, sub-circular in section, rectal furrow weak. Ventral channel narrowly overlapping capsule gland; longitudinal fold weakly developed. Genital aperture a terminal slit, sometimes slightly separated, lacking an anterior expansion. Coiled oviduct a single, tight circular loop, sometimes weakly kinked proximally. Oviduct and bursal duct joining slightly behind pallial wall. Oviduct opening to albumen gland at pallial wall. Bursa copulatrix short, narrow, sub-globular to ovate, longitudinal, with 33–50% of length posterior to gland. Bursal duct originating from anterior edge at mid-line, long, narrow. Seminal receptacle very small, pouchlike, positioned well anterior to bursa near ventral edge of albumen gland.

Testis 1.25 whorls, filling almost all of digestive gland behind stomach, overlapping posterior and part of anterior stomach chambers. Prostate gland very small, ovate, pallial portion short, ovate in section. Proximal pallial vas deferens broadly arched (angling toward rectum). Penis (Figure 33D, E) large; base rectangular, sometimes near square, inner edge weakly folded, often expanded distally; filament medium length, narrow, tapering to point, slightly oblique; lobe slightly shorter than base, broadly triangular, longitudinal. Terminal gland medium-sized, narrow, usually transverse, ventral, but sometimes curving to dorsal surface. Penial gland filling most of length of filament, almost as wide as filament. Ventral gland large, borne on pronounced swelling, traversing penis near base of filament. Penial duct straight, near outer edge.

Type locality: Little Warm Spring, Duckwater Valley, Nye County, Nevada, T. 12 N, R. 56 E, NE ¼ section 5. Holotype, USNM 873191 (Figure 19F), collected by J.J. Landye, 3 September 1973; paratypes, USNM 860712. Snails were collected from rocks in the 1 m deep outflow of this spring.

Remarks: This unusual thermal endemic is not closely similar to other species of the region. Although the penial glands of *P. **villacampae*** conform, in general, to that of widespread *P. kolobensis,* this snail otherwise differs in its broader shell; narrower, more pointed central cusps on the central radular teeth; broader penis, smaller sperm pouches, and more anteriorly positioned seminal receptacle (relative to bursa copulatrix). The distribution of this species is shown in Figure 51.

Material examined: NEVADA. *Nye County:* Little Warm Spring, USNM 860712, USNM 873191, USNM 874759, USNM 892015.—Big Warm Spring, Duckwater Valley (Figure 4D), T. 13 N, R. 56 E, SE ¼ section 32, USNM 883938.

*Pyrgulopsis **anatina*** Hershler, sp. nov.

Southern Duckwater pyrg

(Figures 7H, 19H, I, 33F–H)

Etymology: From *anatinus* (Latin), relating to ducks; referring to endemism of this species in Duckwater Valley.

Diagnosis: Medium-sized, with broadly to ovate-conic shell. Penis medium-sized; filament and lobe medium length. Penial ornament a small terminal gland, and medium-sized penial gland.

Description: Shell (Figures 7H, 19H, I) broadly to ovate-conic, width/height, 71–81%; height, 2.3–2.9 mm; width, 1.8–2.3 mm; whorls, 4.25–4.75. Protoconch 1.25 whorls, diameter 0.35 mm; surface smooth except for very weak wrinkling along inner edge near apex. Teleoconch whorls medium to highly convex, shoulders weakly developed to broad. Aperture ovate, usually adnate, sometimes slightly disjunct. Inner lip complete, slightly thickened, without columellar shelf. Outer lip thin, orthocline or weakly prosocline, without sinuation. Umbilicus rimate to shallowly perforate. Periostracum tan.

Operculum ovate, amber; nucleus slightly darker hue; nucleus eccentric; dorsal surface weakly frilled. Attachment scar thick all around.

Radula 570 × 85 μm, with 59 rows of teeth. Central tooth 22 μm wide, with highly indented dorsal edge; lat-

eral cusps, 6–10; central cusp narrow, dagger- or spoon-like; basal cusps sometimes accompanied by thickening to outside. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 3(4, 5)-1-4(5, 6); neck weakly on medium-flexed; outer wing 180% of cutting edge length. Inner marginal teeth with 25–30 cusps; cutting edge occupying 38% of length of tooth. Outer marginal teeth with 27–42 cusps; cutting edge occupying 26% of length of tooth. Stomach slightly longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles light to medium grey-brown, pigmented often concentrated proximally. Snout light to dark grey-brown, sometimes almost black. Foot light to medium grey-brown. Neck light to medium grey-brown. Pallial roof, visceral coil dark brown-black. Penial filament darkly pigmented except for distalmost portion; black pigment granules scattered on distal penis.

Ctenidial filaments, 22, pleated; ctenidium overlapping pericardium proximally. Osphradium small, narrow, centered posterior to middle of ctenidium. Renal gland longitudinal; kidney opening slightly thickened. Rectum broadly overlapping pallial oviduct, slightly overlapping prostate gland.

Ovary 1.0 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior and part of anterior stomach chamber. Distal female genitalia shown in Figure 33F. Albumen gland having short pallial component. Capsule gland shorter, narrower than albumen gland, sub-circular in section; rectal furrow well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a broad, posterior-oblique loop preceded by well-developed posterior-oblique twist or small coil. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copulatrix medium length and width, ovate or weakly pyriform, longitudinal, with 33% of length posterior to gland. Bursal duct originating from anterior edge at mid-line, short to almost as long as bursa, medium width, sometimes poorly distinguished from bursa. Seminal receptacle small to medium-sized, narrow pouch-shaped, overlapping or lateral to anterior half of bursa.

Testis 1.5 whorls, filling more than 50% of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland bean-shaped, pallial portion medium-large (up to 40%), narrowly ovate in section. Proximal pallial vas deferens having well-developed loop; duct broad. Penis (Figure 33G, H) medium-sized (stunted in parasitized animals); base narrowly rectangular, smooth; filament medium length and width, tapering to point, longitudinal or slightly oblique; lobe slightly shorter to as long as filament, narrow, knoblike, longitudinal. Terminal gland small, ovate, transverse, ventral. Penial gland filling proximal 67% of filament, slightly narrower than filament. Penial duct straight, near outer edge.

Type locality: Spring, southeast of Old Collins Spring, Duckwater Valley, Nye County, Nevada, T. 12 N, R. 56 E, NE ¼ section 20 (Figure 51). Holotype, USNM 883848 (Figure 19H), collected by R. Hershler and P. Hovingh, 12 July 1994; paratypes, USNM 860710. The type locality is a small rheocrene.

Remarks: This species is contrasted with ***P. marcida*** (above) and also with ***P. serrata*** (below). The single sample of this species contained few males, and only one specimen had a fully extended penis.

Material examined: NEVADA. *Nye County:* Spring, southeast of Old Collins Spring, USNM 860710, USNM 883848.

Pyrgulopsis ***planulata*** Hershler, sp. nov.

Flat-topped Steptoe pyrg

(Figures 7I, 13B, 15A–C, 19J, 34A–C)

Etymology: From *planus* (Latin), flat; *ulus*, diminutive suffix; referring to the small sub-discoidal shell of this species.

Diagnosis: Small, with highly eroded shell apex, remaining portion sub-globular to discoidal. Penis medium-sized, filament medium length, lobe very short. Penial ornament of small terminal gland, very small Dg1, and small Dg2.

Description: Shell (Figures 7I, 19J) apex highly eroded, remaining portion sub-globular to discoidal, width/height, 92–108%; height, 1.1–1.4 mm; width, 1.1–1.5 mm; whorls, 2.0–3.0. Protoconch eroded. Body whorl medium convexity, sometimes weakly angulate below periphery, shoulder weakly developed. Aperture ovate, weakly angled above; usually adnate, larger specimens sometimes slightly disjunct. Inner lip slightly thickened in larger specimens; columellar shelf often covering most of umbilical region. Outer lip thin (slightly thickened in larger specimens), strongly prosocline, without sinuation. Shell anomphalous or with narrowly rimate umbilicus; umbilical region sometimes narrowly excavated. Periostracum tan.

Operculum (Figure 13B) broadly ovate, multispiral, amber, nuclear region reddish; nucleus eccentric; dorsal surface frilled. Attachment scar thick along most of perimeter; whorl edges bulging.

Radula (Figure 15A–C) 550 × 90 μm, with 65 rows of teeth. Central tooth 16 μm wide, with highly indented dorsal edge; lateral cusps, 3–6 (dorsally fused); central cusps broad, daggerlike (often with jagged edge), basal cusps absent, although small swelling often present in area. Basal tongue V-shaped, longer than lateral angles, basal sockets shallow. Lateral margins narrow, strongly flared. Lateral tooth formula 4(5)-1-4(5); neck well flexed; outer wing 260% of cutting edge length. Inner marginal teeth with 24–26 cusps; cutting edge occupying 28% of length of tooth. Outer marginal teeth with 27–30

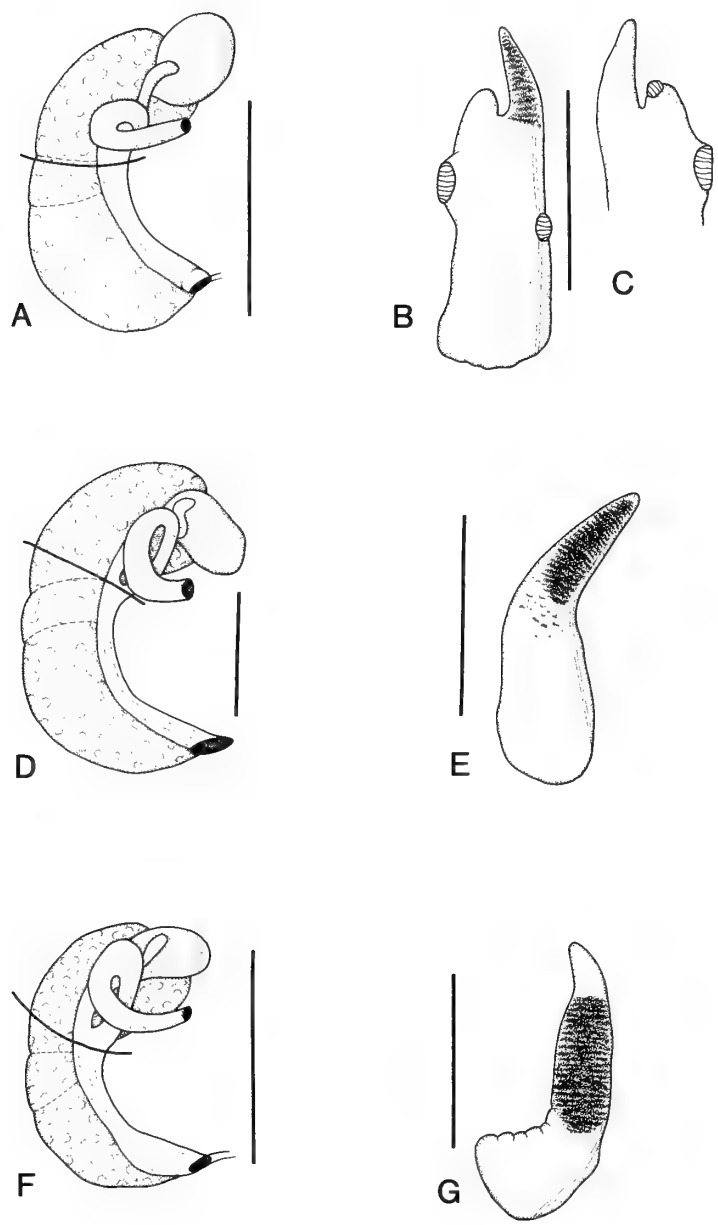


Figure 34

Genitalia of *Pyrgulopsis* species (A–C, *P. **planulata,*** USNM 860686; D, E, *P. **sulcata,*** USNM 860683; F, G, *P. **orbiculata,*** USNM 860682). A–C. Bars = 0.5 mm. D. Bar = 0.25 mm. E. Bar = 0.5 mm. F. Bar = 0.5 mm. G. Bar = 0.25 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis (not shown for *P. **sulcata*** and *P. **orbiculata*** as penial ornament absent).

cusps; cutting edge occupying 20% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles, snout dark brown. Foot, neck medium to dark brown. Opercular lobe dark along inner edge, often all around, central zone unpigmented. Pallial roof, visceral coil uniform black. Penial filament darkly pigmented internally along most of length; portion of base adjacent to filament lightly to darkly pigmented.

Ctenidial filaments, 13; ctenidium connected to pericardium by short efferent vein. Osphradium small, narrow, positioned posterior to middle of ctenidium. Renal gland slightly oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.5 whorl, filling more than 50% of digestive gland behind stomach, slightly overlapping posterior stomach chamber. Distal female genitalia shown in Figure 34A. Albumen gland without pallial component. Capsule gland longer and as wide as albumen gland, having short pallial component, sub-globular in section, rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a short, terminal slit, mounted on weakly raised papilla, with short anterior extension. Coiled oviduct a tight circular or posterior-oblique loop. Oviduct and bursal duct joining just behind pallial wall. Bursa copulatrix medium length and width, ovate, usually longitudinal (sometimes oblique), 50–67% of length posterior to gland. Bursal duct originating from anterior edge at or near mid-line, medium length and width. Seminal receptacle small, pouchlike, often folded, overlapping anterior portion of bursa.

Testis 0.75–1.0 whorl, filling almost all of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland broadly ovate, pallial portion short, ovate in section. Proximal pallial vas deferens weakly looped. Penis (Figure 34B, C) medium-sized; base rectangular, weakly folded or smooth; filament medium length and width, tapering to point, longitudinal; lobe very short, longitudinal or slightly oblique, narrowly rounded. Terminal gland small, ovate, transverse, ventral. Dg1 very small, ovate, slightly raised, longitudinal, positioned along inner edge medially. Dg2 small, ovate, borne on distal expansion or lobelike swelling (lateral to edge of penis), positioned slightly proximal to lobe, largely or entirely ventral. Penial duct straight, very close to outer edge.

Type locality: Spring, northwest of Clark Spring, Steptoe Valley, White Pine County, Nevada, T. 19 N, R. 63 E, NW ¼ section 20 (Figure 51). Holotype, USNM 892023 (Figure 19J), collected by R. Hershler and P. Hovingh, 9 May 1995; paratypes, USNM 860686. The type locality is one of a series of small, thermal (23.3°C.) rheocrenes which enter an irrigation ditch on a private ranch. These springs also harbor an undescribed species of *Tryonia.*

Remarks: This snail and four other species are locally endemic to a large wetland near the southeast corner of Steptoe Valley. These species share numerous unusual features suggesting that they compose a local radiation, including small size, squat shell with columellar shelf and/or excavated umbilical region, strong protoconch sculpture, frilled operculum; deeply notched central radular teeth with attenutate, flared margins, long basal tongue, shallow sockets, fused lateral cusps, broad central cusps; long wings on lateral teeth, short cutting edges of marginal teeth, well posterior position of bursa copulatrix, simple oviduct coil, and capsule gland opening frequently developed as a papilla. *Pyrgulopsis* ***planulata*** differs from other members of this group by its unique pattern of penial ornament, consisting of small terminal gland, Dg1 and Dg2.

Material examined: NEVADA. *White Pine County:* Spring, northwest of Clark Spring, USNM 860686, USNM 883985, USNM 892023, USNM 892026.

Pyrgulopsis ***sulcata*** Hershler, sp. nov.

Southern Steptoe pyrg

(Figures 7J, 11F, 19K, 34D, E)

Etymology: From *sulcatus* (Latin), furrowed; referring to the excavated shell umbilical region typical of this species.

Diagnosis: Small, with low-trochoid to ovate-conic shell. Penis medium-sized, bladelike, filament medium length, lobe absent. Penial ornament absent.

Description: Shell (Figures 7J, 19K) low trochoid to ovate conic, apex usually eroded, parasitized specimens often cylindrical, width/height, 79–91%; height, 1.2–1.4 mm; width, 1.0–1.2 mm; whorls, 4.0–4.5. Protoconch (Figure 11F) 1.1 whorls, diameter 0.24 mm, coarsely wrinkled, with sculpture weakening slightly near teleoconch border. Teleoconch whorls weakly convex, shoulders well developed, narrow. Aperture ovate, adnate. Inner lip complete, slightly thickened, often having narrow columellar shelf. Outer lip thin, prosocline, without sinuation. Umbilicus absent or rimate; umbilical region often excavated and bordered by adaxial ridge. Periostracum light tan.

Operculum ovate, reddish; nucleus eccentric; dorsal surface weakly frilled near inner edge. Attachment scar broadly thickened between nucleus and inner edge.

Radula 420 × 66 μm, with 73 rows of teeth. Central tooth 11 μm wide, with highly indented dorsal edge; lateral cusps, 4–7, often fused dorsally; central cusp narrow, daggerlike; basal cusps usually absent, sometimes present as very small, nublike vestiges. Basal tongue V-shaped, extending well below lateral angles; basal sockets shallow. Lateral margins very narrow, strongly flared. Lateral tooth formula 5(6)-1-6(7); neck weakly flexed; outer wing 250% of cutting edge length. Inner marginal teeth with 27–30 cusps; cutting edge occupying 33% of length of tooth. Outer marginal teeth with 26–28 cusps; cutting edge occupying 23% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum very small.

Cephalic tentacles unpigmented to medium grey-brown. Snout medium to dark grey-brown. Foot light to medium grey-brown. Opercular lobe dark along inner edge, sometimes all around. Neck unpigmented to medium grey-brown. Pallial roof, visceral coil uniformly black. Penial filament darkly pigmented internally, pigment usually also present on distal portion of base.

Ctenidium narrow; filaments, 11, without pleats; cte-

nidium connected to pericardium by short efferent vessel. Osphradium small, narrow, positioned alongside posterior half of ctenidium. Renal gland oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.75–1.0 whorl, filling 50% of digestive gland behind stomach, abutting or slightly overlapping posterior stomach chamber. Distal female genitalia shown in Figure 34D. Pallial albumen gland very short or absent. Capsule gland longer, narrower than albumen gland, sub-circular in section, proximal section well posterior; rectal furrow well developed. Ventral channel slightly overlapping capsule gland; longitudinal fold weakly developed. Genital aperture a terminal slit, loosened from capsule gland, almost papillalike, anterior extension absent. Coiled oviduct a tight circular or narrow U-shaped loop. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, ovate, longitudinal or slightly oblique (anterior edge dorsal), with short section posterior to gland. Bursal duct originating from anterior edge at mid-line, slightly shorter than bursa, medium width, slightly embedded in albumen gland. Seminal receptacle small, narrow, sometimes folded, overlapping anterior portion of bursa.

Testis 1.0 whorl, filling 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Prostate gland bean-shaped, pallial portion medium, narrowly ovate in section. Proximal pallial vas deferens straight or with weak bend or undulation. Penis (Figure 34E) medium-sized; base narrowly rectangular, lacking folds, weakly distinguished distally from filament; filament slightly shorter and narrower than base, tapering to rounded tip, longitudinal or slightly oblique; lobe and glands absent. Penial duct straight, very close to outer edge.

Type locality: Springs, north of Grass Springs, Steptoe Valley, White Pine County, Nevada, T. 19 R, R. 63 E, NW ¼ section 8. Holotype, USNM 874326 (Figure 19K), collected by R. Hershler, 5 August 1991; paratypes, USNM 860683. The type locality is a small, marshy rheocrene whose outflow has been dug out to form a canal (Figure 4E).

Remarks: This snail closely resembles *P. **orbiculata*** (described below), which occurs just to the north, but its shell has less rounded whorls with deeper sutures, stronger shoulders, and a broader columellar shelf. In addition, *P. **sulcata*** differs in the nearly smooth dorsal surface of the operculum, weaker development of basal cusps on the central radular teeth, and shorter penial filament. The distribution of this species is shown in Figure 51.

Material examined: NEVADA. *White Pine County:* Springs, north of Grass Springs (Figure 4E), USNM 860683, USNM 874326.—Spring, northwest of Clark Spring, Steptoe Valley, T. 19 N, R. 63 E, NW ¼ section 20, USNM 883427, USNM 883894, USNM 892022.

*Pyrgulopsis **orbiculata*** Hershler, sp. nov.

Sub-globose Steptoe Ranch pyrg

(Figures 7K, 19L, 34F, G)

Etymology: From *orbis* (Latin), circle (coupled with diminutive suffix); referring to the small, sub-globose shell of this species.

Diagnosis: Small, with globose shell. Penis small, bladelike; filament long, lobe absent. Penial ornament absent.

Description: Shell (Figures 7K, 19L) sub-globose, width/height, 81–96%; height, 1.1–1.3 mm; width, 1.0–1.2 mm; whorls, 3.75–4.25. Protoconch 1.2–1.25 whorls, diameter 0.25 mm, coarsely wrinkled, with sculptured weakening slightly near teleconch boundary. Teleoconch whorls highly convex, often weakly angled at the periphery, shoulders absent or weak and narrow. Aperture broadly ovate, angled above, usually adnate. Inner lip slightly thickened, usually having narrow columellar shelf. Outer lip thin, prosocline, without sinuation. Umbilicus rimate to perforate, sometimes narrowly excavated. Periostracum tan.

Operculum ovate, amber, reddish in nuclear region; nucleus eccentric; dorsal surface strongly frilled; outer margin smooth. Attachment scar thick almost all around; whorl edges slightly bulging.

Radula 720 × 114 μm, with 75 rows of teeth. Central tooth 12 μm wide, with highly indented dorsal edge; lateral cusps, 4–6 (often fused dorsally); central cusp narrow, daggerlike; basal cusps small, weakly developed. Basal tongue V-shaped, longer than lateral margins, basal sockets shallow. Lateral margins very narrow, strongly flared. Lateral tooth formula 5-1-6(7); neck weakly flexed; outer wing 290% of cutting edge length. Inner marginal teeth with 27–29 cusps; cutting edge occupying 33% of length of tooth. Outer marginal teeth with 23–30 cusps; cutting edge occupying 22% of length of tooth. Stomach longer than style sac; anterior stomach chamber larger than posterior chamber, stomach caecum very small.

Cephalic tentacles light to medium brown. Snout, foot medium to dark brown. Opercular lobe medium to dark along outer edge. Neck unpigmented to medium brown. Pallial roof, visceral coil uniformly dark brown. Penial filament darkly pigmented internally for most of length; pigment often extending onto distal penis.

Ctenidial filaments, 11, without pleats, ctenidium connected to pericardium by short efferent vessel. Osphradium medium-sized (40–50%), narrow, positioned slightly posterior to middle of ctenidium. Renal gland oblique; kidney opening grey-white. Rectum broadly overlapping glandular oviduct, abutting or slightly overlapping prostate gland.

Ovary 0.75–1.0 whorl, filling 50% of digestive gland behind stomach, overlapping posterior stomach chamber.

Distal female genitalia shown in Figure 34F. Albumen gland having very short pallial component. Capsule gland slightly longer, but narrower than albumen gland, subcircular in section; rectal furrow well developed. Ventral channel slightly overlapping capsule gland proximally, broadening distally; longitudinal fold weakly developed. Genital aperture a terminal slit, slightly raised distally, having short anterior extension. Coiled oviduct a single circular to posterior-oblique loop. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copulatrix medium length and width, ovate, longitudinal, up to 50% of length posterior to gland. Bursal duct originating from anterior edge, slightly shorter to as long as bursa, medium width. Seminal receptacle small, pouchlike, overlapping anterior half of bursa, sometimes extending to edge of albumen gland.

Testis 1.0 whorl, filling 50% of digestive gland behind stomach, overlapping both stomach chambers anteriorly. Prostate gland bean-shaped, pallial portion very short, ovate in section. Proximal pallial vas deferens having U-shaped bend (toward ctenidium). Penis (Figure 34G) small, bladelike; base near square, folded along inner edge; filament poorly distinguished from base, but apparently long, slightly narrower than base, tapering to rounded tip, longitudinal; lobe and glands absent. Penial duct straight, very close to outer edge.

Type locality: Spring, Steptoe Ranch, Steptoe Valley, White Pine County, Nevada, T. 19 N, R. 63 E, SW ¼ section 5. Holotype, USNM 873196 (Figure 19L), collected by J. J. Landye, 1 September 1980; paratypes, USNM 860682. The type locality is a small rheocrene adjacent to an old ranch house.

Remarks: This species is contrasted with *P.* ***sulcata*** above. The distribution of this snail is shown in Figure 51.

Material examined: NEVADA. *White Pine County:* Springs, Steptoe Ranch, USNM 860682, USNM 873196, USNM 892015.—Springs, ca. 1.6 km north-northwest of Steptoe Ranch, Steptoe Valley, T. 19 N, R. 63 E, NW ¼ section 5, USNM 873195.

Pyrgulopsis ***neritella*** Hershler, sp. nov.

Neritiform Steptoe Ranch pyrg

(Figures 7L, 11G, 20A, 35A, B)

Etymology: From *nerita* (Latin), sea-snail (dim.); referring to the small, neritiform shell of this species.

Diagnosis: Small; with apically eroded neritiform shell. Penis small, filament long, lobe absent. Penial ornament a large Dg1.

Description: Shell (Figures 7L, 11G) neritiform, apex invariably eroded, width\height, 77–100%; height, 1.1–1.7 mm; width, 1.0–1.5 mm; whorls, about 3.5. Protoconch (Figure 11G) 1.25 whorls, diameter 0.27 mm; strongly wrinkled, although sculpture weakening near teleoconch border. Teleoconch whorls moderately convex, strongly shouldered, usually bearing well developed sub-sutural cord or welt. Aperture broadly ovate, angled above, broadly adnate, sometimes having adapical portion loosened from body whorl. Inner lip thin, having broad columellar shelf (covering umbilical region). Outer lip thin, strongly prosocline, without sinuation. Umbilicus absent or narrowly rimate; umbilical region sometimes narrowly excavated. Periostracum light brown.

Operculum ovate, reddish; nucleus highly eccentric; dorsal surface smooth. Attachment scar thick all around.

Radula 530 × 80 μm, with 80 rows of teeth. Central tooth 13 μm wide, with highly indented dorsal edge; lateral cusps, 2–4 (most of cusp row completely fused dorsally); central cusp broad, having bifurcate or jagged edge; basal cusps absent, although region occasionally having very slight thickenings. Basal tongue V-shaped, longer than lateral margins, basal sockets shallow. Lateral margins very narrow. Lateral tooth formula 4-1-4(5); neck weakly flexed; outer wing 310% of cutting edge length. Inner marginal teeth with 26–30 cusps; cutting edge occupying 32% of length of tooth. Outer marginal teeth with 28–32 cusps; cutting edge occupying 21% of length of tooth. Stomach longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles, snout, foot medium to dark brown. Opercular lobe dark along inner edge, sometimes all around. Neck unpigmented to medium brown. Pallial roof, visceral coil uniformly dark brown. Penial filament darkly pigmented internally; pigment often extending into proximal portion of base.

Ctenidium narrow; filaments, 12, without pleats, slightly overlapping pericardium posteriorly. Osphradium small, narrowly ovate, positioned slightly posterior to middle of ctenidium. Renal gland oblique; kidney opening grey-white. Rectum broadly overlapping pallial oviduct, slightly overlapping prostate gland.

Ovary 0.5 whorl, filling 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 35A. Albumen gland without a pallial component. Capsule gland slightly longer but narrower than albumen gland, sub-circular in section, without anterior extension; rectal furrow well developed. Ventral channel narrowly overlapping capsule gland; longitudinal fold weakly developed. Genital aperture a terminal pore borne on weak papilla extending distally to capsule gland. Coiled oviduct a single tight circular or posterior-oblique loop, sometimes kinked at mid-length. Oviduct and bursal duct joining just behind pallial wall. Bursa copulatrix slightly shorter and narrower than albumen gland, broadly ovate, longitudinal, 50% of length posterior to gland. Bursal duct originating from

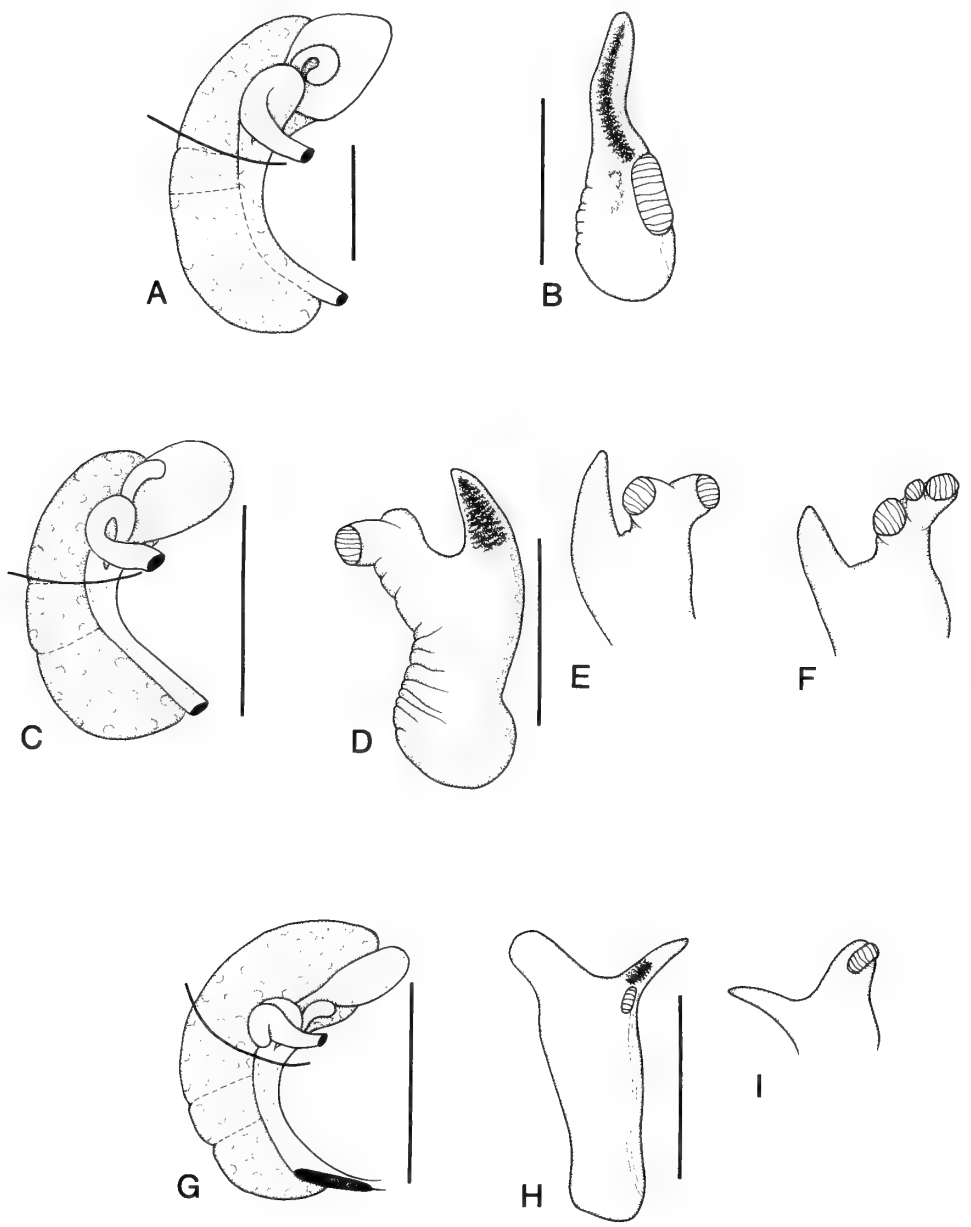


Figure 35

Genitalia of *Pyrgulopsis* species (A, B, ***P. neritella,*** USNM 860684; C–F, ***P. landyei,*** USNM 860685; G–I, ***P. serrata,*** USNM 860719). A, B. Bars = 0.25 mm. C–I. Bars = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis (not shown for ***P. neritella*** as ventral ornament absent).

anterior edge at mid-line, short, medium width. Seminal receptacle small, narrow, often coiled, overlapping anterior portion of bursa.

Testis 1.0 whorl, filling almost all of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland elongate bean-shaped, pallial portion large (50%), ovate in section. Proximal pallial vas deferens straight or weakly bent. Penis (Figure 35B) small; base near square, poorly distinguished from filament, inner edge weakly folded; filament as long as and almost as wide as base, weakly tapered, longitudinal; lobe absent. Dg1, large, broad, sometimes slightly raised, borne along outer edge just proximal to filament. Penial duct straight, near outer edge.

Type locality: Springs, north of Steptoe Ranch, Steptoe Valley, White Pine County, Nevada, T. 19 N, R. 63 E, SW ¼ section 5. Holotype, USNM 883932 (Figure 20A), collected by R. Hershler and P. Hovingh, 9 May 1995; paratypes, USNM 860684. The type locality is a series of thermal (23°C.) rheocrenes whose outflows enter an impoundment on a privately owned ranch. This site also harbors an undescribed species of *Tryonia.*

Remarks: This species is distinguished from other taxa found in southeast Steptoe Valley by its neritiform shell, pattern of penial ornamentation (consisting solely of a prominent Dg1), and distally extended and weakly papillate capsule gland opening. The distribution of this species is shown in Figure 51.

Material examined: NEVADA. *White Pine County:* Spring, north of Steptoe Ranch, USNM 860684, USNM 873194, USNM 883932.—Springs, just north of above, Steptoe Valley, T. 19 N, R. 63 E, SW ¼ section 5, USNM 883936.

Pyrgulopsis ***landyei*** Hershler, sp. nov.

Landyes pyrg

(Figures 8A, 20B, 35C–F)

Etymology: Named after J. Jerry Landye, in recognition of his long-term efforts to document and conserve aquatic mollusks in the western United States.

Diagnosis: Small, with broadly conical shell. Penis large, filament medium and lobe length. Penial ornament a large, fragmented terminal gland.

Description: Shell (Figures 8A, 20B) broadly conical, but apex invariably eroded, yielding a globular appearance, width/height, 83–98%; height, 1.3–1.7 mm; width, 1.3–1.7 mm; whorls, 3.0–4.25. Protoconch 1.25 whorls, diameter 0.27 mm, initial 0.75 whorl coarsely wrinkled, remaining portion finely wrinkled. Teleoconch whorls highly convex, shoulders well developed. Aperture broadly ovate, usually broadly adnate, rarely slightly disjunct. Inner lip thin, columellar shelf medium width. Outer lip thin, strongly prosocline, without sinuation. Umbilicus anomphalous or narrowly rimate; umbilical region sometimes narrowly excavated. Periostracum tan.

Operculum ovate, reddish; nucleus eccentric; dorsal surface frilled. Attachment scar thick all around; whorl edges sometimes slightly bulging.

Radula 550 × 80 μm, with 68 rows of teeth. Central tooth 15 μm wide, with highly indented dorsal edge; lateral cusps, 2–4 (cusp edge strongly fused dorsally); central cusp broad, triangular; basal cusps absent, although sometimes a weak swelling present. Basal tongue V-shaped, longer than lateral angles, basal sockets shallow. Lateral margins narrow, strongly flared. Lateral tooth formula 4(5)-1-3(4, 5); neck weakly flexed; outer wing 250% of cutting edge length. Inner marginal teeth with 25–27 cusps; cutting edge occupying 29% of length of tooth. Outer marginal teeth with 27–32 cusps; cutting edge occupying 22% of length of tooth. Stomach longer than style sac; stomach chambers equal-sized; stomach caecum small.

Cephalic tentacles medium to dark brown. Snout, foot dark brown. Opercular lobe dark along inner edge, sometimes all around. Neck medium grey-brown. Pallial roof, visceral coil uniform dark brown to black. Penial filament darkly pigmented along most of length; black granules also scattered on base.

Ctenidial filaments, 13, without pleats, ctenidium connected to pericardium by short efferent vessel. Osphradium small, narrow, positioned centrally or slightly posterior to middle of ctenidium. Renal gland longitudinal or slightly oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.75 whorl, filling more than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 35C. Albumen gland with extremely short or no pallial component. Capsule gland slightly longer and as wide as albumen gland, sub-globose in section; rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold weakly developed. Genital aperture a terminal slit mounted on a weak papilla, without anterior extension. Coiled oviduct a posterior-oblique loop sometimes preceded by posterior-oblique twist. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length, slightly narrower to as wide as albumen gland, broadly ovate, longitudinal, with 50–75% of length posterior to gland. Bursal duct originating from anterior edge at mid-line, short, medium width, proximal portion often looping. Seminal receptacle small, pouch-like, often coiled, overlapping anterior portion of bursa.

Testis 1.0 whorl, filling more than 50% of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland bean-shaped, pallial portion medium, ovate in section. Proximal pallial vas having well-developed loop. Penis (Figure 35D–F) large; base rectangular, inner edge folded; filament medium length and width, tapering to point, longitudinal; lobe as long as filament, clublike, often distally bifurcate, slightly oblique. Terminal gland large, composed of two circular units borne on edges of distally bifurcate lobe; one to two smaller, but similarly circular units sometimes present, positioned between main glands. (Lobe rarely simple, with single terminal gland.) Occasional specimens having dotlike or narrow, distal Dg2. Penial duct straight, very close to outer edge.

Type locality: Spring, ca. 1.6 km north-northwest of Steptoe Ranch, Steptoe Valley, White Pine County, Nevada, T. 19 N, R. 63 E, NW ¼ section 5 (Figure 51). Holotype, USNM 892014 (Figure 20B), collected by J. Landye, 21 November 1995; paratypes, USNM 860685. The type locality is a small rheocrene whose headspring is protected by an old fence.

Remarks: This species differs from others found in southeast Steptoe Valley in having a well-developed penial lobe and penial ornament consisting of a bifurcate terminal gland.

Material examined: NEVADA. *White Pine County:* Spring, ca. 1.6 km north-northwest of Steptoe Ranch, USNM 860685, USNM 892012, USNM 892014.

Pyrgulopsis ***serrata*** Hershler, sp. nov.

Northern Steptoe pyrg

(Figures 8B, 15D–F, 20C–E, 35G–J)

Etymology: From *serratus* (Latin), toothed like a saw; referring to the numerous cusps on the radular teeth of this species.

Diagnosis: Medium-sized, with ovate- to narrow-conic shell. Penis medium-sized, filament and lobe medium length. Penial ornament of small terminal and penial glands.

Description: Shell (Figures 8B, 20C–E) ovate- to narrow-conic (almost turriform), width/height, 56–87%; height, 2.0–4.1 mm; width, 1.5–2.6 mm; whorls, 4.0–5.25. Protoconch 1.3 whorls, diameter 0.33 mm, initial 0.75 whorl finely wrinkled (stronger along inner edge), later portion near smooth. Teleoconch whorls moderately to highly convex, shouldered. Aperture ovate, narrowly adnate or slightly disjunct. Inner lip sometimes thick, without columellar shelf. Outer lip thin or thick, prosocline, without sinuation. Umbilicus rimate to perforate; umbilical region often narrowly excavated. Periostracum tan.

Operculum ovate, amber, reddish in nuclear region; nucleus eccentric; dorsal surface frilled; outer margin sometimes having weak rim. Attachment scar slightly thickened between nucleus and inner edge, sometimes similarly thick all around.

Radula (Figure 15D–F) 860 × 148 μm, with 67 rows of teeth. Central tooth 18 μm wide, with highly indented dorsal edge; lateral cusps, 7–9; central cusp medium width, daggerlike; basal cusps large. Basal process V-shaped, basal sockets medium depth. Lateral tooth formula 4(5)-1-4(6); neck weakly flexed; outer wing 215% of cutting edge length. Inner marginal teeth with 29–33 cusps; cutting edge occupying 33% of length of tooth. Outer marginal teeth with 31–33 cusps; cutting edge occupying 25% of length of tooth. Stomach and style sac equal in length; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented (except for short stripe just distal to eyes) to medium grey. Snout, foot unpigmented to medium grey. Opercular lobe dark along inner edge, sometimes pigmented all around. Neck unpigmented or light grey. Pallial roof, visceral coil uniform black. Proximal portion to entire penial filament darkly pigmented internally.

Ctenidium narrow; filaments, 14, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrowly ovate, positioned slightly posterior to middle of ctenidium. Renal gland oblique; kidney opening grey-white. Rectum broadly overlapping pallial oviduct, slightly overlapping prostate gland.

Ovary 0.5 whorl, filling less than 50% of digestive gland behind stomach, slightly overlapping posterior stomach chamber anteriorly. Distal female genitalia shown in Figure 35G. Albumen gland having 33% of length in pallial cavity. Capsule gland shorter and narrower than albumen gland, sub-circular in section; rectal furrow very weak. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit with short anterior extension. Coiled oviduct of two small, overlapping, posterior oblique loops. Oviduct and bursal duct joining just behind pallial wall. Bursa copulatrix short, narrow, narrowly ovate, positioned near ventral edge of albumen gland, longitudinal, with 50% of length posterior to gland. Bursal duct originating from anterior edge at mid-line, slightly shorter to as long as bursa, medium width. Seminal receptacle small, narrow, overlapping or ventral to anteriormost portion of bursa or proximal bursal duct.

Testis 1.0–1.25 whorls, filling almost all of digestive gland behind stomach, overlapping posterior and small part of anterior stomach chamber. Prostate gland very small, ovate, pallial portion short, narrowly ovate in section. Proximal pallial vas deferens having well-developed bend (often slightly reflexed). Penis (Figure 35H, I) medium-sized; base rectangular, lacking folds; filament slightly shorter than base, tapering to point, medium width, slightly oblique; lobe slightly longer than filament, knoblike, slightly oblique. Terminal gland small, narrow, ventral, nearly longitudinal. Penial gland small, rarely medium-sized, sometimes minute or absent in stunted penes, slightly narrower to as wide as filament, sometimes raised, positioned near base of filament (sometimes slightly overlapping base). Penial duct straight, near outer edge.

Type locality: Indian Ranch Spring, Steptoe Valley, White Pine County, Nevada, T. 26 N, R. 63 E, NE ¼ section 20. Holotype, USNM 874314 (Figure 20C), collected by R. Hershler, 4 August 1991; paratypes, USNM 860719. The type locality is a shallow, but broad (>30 m) rheocrene coursing down a forested mountain slope.

Remarks: Among the group of species having penial ornament solely consisting of a terminal gland and small penial gland, *P.* ***serrata*** most closely resembles *P.* ***anatina,*** from Railroad Valley. *Pyrgulopsis* ***serrata*** differs from *P.* ***anatina*** in having a longitudinal (not transverse) terminal gland and smaller penial gland. The distribution of *P.* ***serrata*** is shown in Figure 51.

Material examined: NEVADA. *Elko County:* Twin Springs, Steptoe Valley, T. 29 N, R. 63 E, NE ¼ section

35, USNM 874318.—Springs, south of Currie, Steptoe Valley, T. 27 N, R. 64 E, NW ¼ section 10, USNM 874312. *White Pine County:* Indian Ranch Spring, USNM 860719, USNM 874314.—Indian Creek, Steptoe Valley, T. 26 N, R. 64 E, section 20, USNM 858018.

Pyrgulopsis ***cruciglans*** Hershler, sp. nov.

Transverse gland pyrg

(Figures 8C, 20F–H, 36A, B)

Etymology: From *crux* (Latin), cross; and *glans,* acorn or gland; referring to the prominent transverse dorsal gland (Dg1) on the penis of this species.

Diagnosis: Small to medium-sized, with ovate- to narrow-conic shell. Penis medium-sized, filament medium length, lobe long. Penial ornament a large Dg1.

Description: Shell (Figures 8C, 20F–H) ovate- to narrow-conic, width/height, 71–85%; height, 1.6–2.7 mm; width, 1.3–2.1 mm; whorls, 4.0–4.75. Protoconch 1.25 whorls, diameter 0.29 mm, surface smooth except for weak wrinkling around edges of apex. Teleoconch whorls moderately convex, weakly shouldered. Aperture ovate, narrowly adnate to slightly disjunct. Inner lip slightly thickened, without columellar shelf. Outer lip thin, slightly prosocline, without sinuation. Umbilicus rimate or perforate. Periostracum tan-brown, often covered with thick brown deposits.

Operculum ovate, amber; nucleus eccentric; dorsal surface frilled; outer margin sometimes having weak rim. Attachment scar thick, sometimes greatly so, along most of perimeter (except for portion of outer edge).

Radula 820 × 130 μm, with 65 rows of teeth. Central tooth 17 μm wide, with medium indented dorsal edge; lateral cusps, 6–7; central cusp narrow, daggerlike; basal cusps medium-sized. Basal process V-shaped, basal sockets medium depth. Lateral tooth formula 4(5)-1-4(5); neck weakly flexed; outer wing 230% of cutting edge length. Inner marginal teeth with 24–27 cusps; cutting edge occupying 30% of length of tooth. Outer marginal teeth with 30–32 cusps; cutting edge occupying 25% of length of tooth. Stomach longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented to light grey. Snout light to medium grey-brown. Foot unpigmented to light grey. Opercular lobe light grey to black along inner edge. Neck light grey. Pallial roof, visceral coil uniform black. Penial filament darkly pigmented internally for most of length; lobe, especially distal portion, containing scattered black granules.

Ctenidial filaments, 15, weakly pleated; ctenidium overlapping pericardium posteriorly. Renal gland slightly oblique; kidney opening grey-white. Rectum broadly overlapping pallial oviduct, slightly overlapping prostate gland.

Ovary 0.5–0.75 whorl, filling 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 36A. Albumen gland having very short pallial component. Capsule gland slightly shorter and narrower than albumen gland, ovate in section; rectal furrow weakly developed. Ventral channel slightly overlapping capsule gland; longitudinal fold weakly developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a posterior-oblique to horizontal loop preceded by well-developed twist or small coil. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, broadly-ovate to sub-globular, longitudinal, with 50–67% of length posterior to gland. Bursal duct originating from anterior edge at mid-line, 50% to almost as long as bursa, medium width. Seminal receptacle small, pouchlike to narrow, overlapping anterior portion of bursa.

Testis 1.0 whorl, filling more than 50% of digestive gland behind stomach, overlapping posterior and small portion of anterior stomach chambers. Prostate gland broadly ovate, pallial portion short, narrowly ovate in section. Proximal pallial vas deferens having well-developed, reflexed bend. Penis (Figure 36B) medium-sized; base nearly square, weakly folded along inner edge; filament slightly shorter than base, narrow, tapering to pointed tip, longitudinal; lobe as long or longer than base; tapering to rounded tip, sometimes greatly narrowed distally, longitudinal. Dg1 large, rarely divided into two units; borne on fleshy pedicel, transverse, positioned slightly proximal to filament. Weak, dotlike Dg3 seen in one specimen. Ventral surface sometimes bearing central swelling, but lacking gland(s). Penial duct straight, near outer edge.

Type locality: Flat Spring, Steptoe Valley, White Pine County, Nevada, T. 25 N, R. 66 E, SE ¼ section 2, collected by R. Hershler, 5 August 1991. Holotype, USNM 874285 (Figure 20F), collected by R. Hershler; 5 August 1991; paratypes, USNM 860709. The type locality is a shallow, broad (13 m) rheocrene which has been dug out and impounded.

Remarks: This species is distinguished from other congeners by its unique penial ornament, which consists solely of a very large, transverse Dg1 borne on a prominent swelling. *Pyrgulopsis* ***cruciglans*** also has an unusually broad oviduct coil. The distribution of this species is shown in Figure 52.

Material examined: NEVADA. *White Pine County:* Flat Spring, USNM 860709, USNM 874285. *Elko County:* Boone Spring, Antelope Valley, T. 27 N, R. 67 E, SE ¼ section 29, USNM 874327.—Dolly Varden Spring, Antelope Valley, T. 28 N, R. 67 E, NW ¼ section 9, USNM 874335.—Ferguson Springs, Great Salt Lake Basin, T. 30 N, R. 69 E, NE ¼ section 33, USNM 874331.

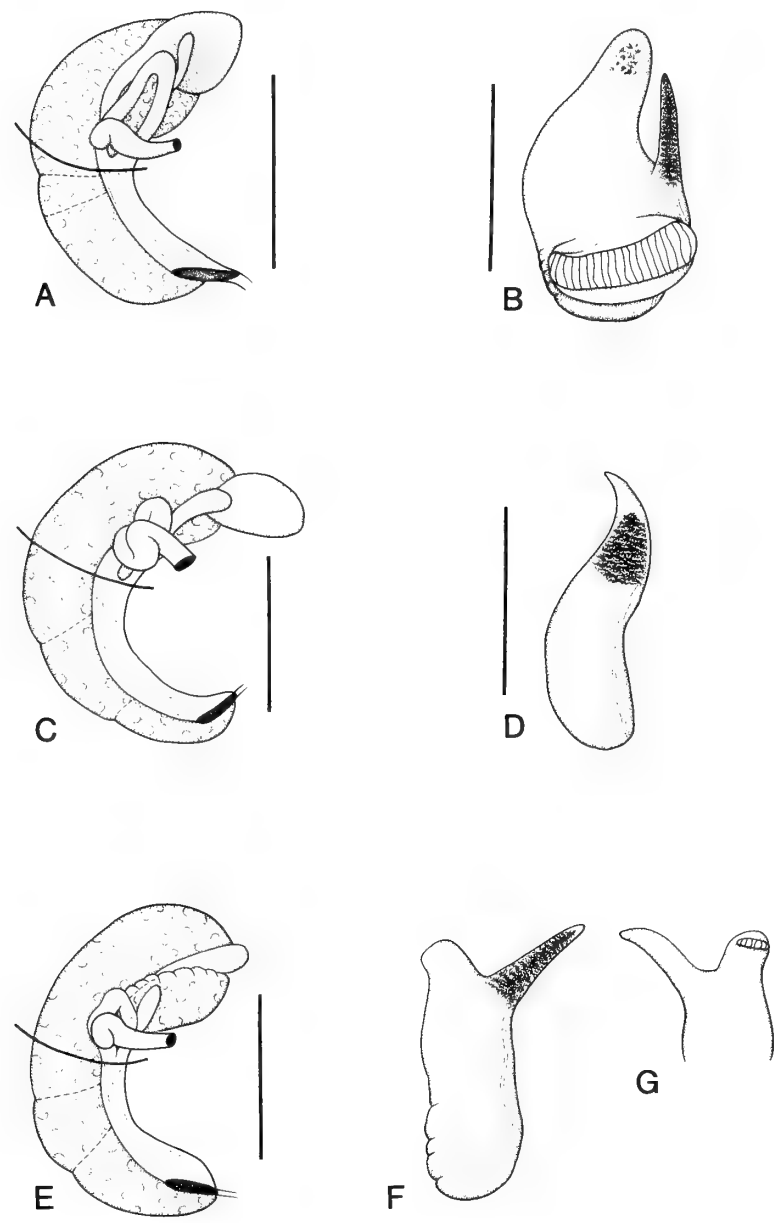


Figure 36

Genitalia of *Pyrgulopsis* species (A, B, *P.* ***cruciglans,*** USNM 860709; C, D, *P.* ***dixensis,*** USNM 860688; E-G, *P.* ***aurata,*** USNM 860696). A, B. Bars = 0.5 mm. C, D. Bars = 0.25 mm. E-G. Bar = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis (not shown for *P.* ***dixensis*** and *P.* ***aurata*** as penial ornament absent on the ventral surface in these species).

Pyrgulopsis ***dixensis*** Hershler, sp. nov.

Dixie Valley pyrg

(Figures 8D, 13C, 20I, J, 36C, D)

Etymology: Referring to endemism of this species in Dixie Valley, Nevada.

Diagnosis: Small, with elongate-conic shell. Penis small, bladelike; filament medium length, lobe absent. Penial ornament absent.

Description: Shell (Figures 8D, 20I, J) elongate-conic, width/height, 48–56%; height, 1.6–2.0 mm; width, 0.8–1.0 mm; whorls, 5.0–5.75. Protoconch 1.25 whorls, diameter 0.28 mm, weakly wrinkled at apex, otherwise smooth. Early teleoconch whorls highly convex, later whorls near flat to

medium convexity, often strongly angled below periphery; shoulder often well developed, but narrow; body whorl often slightly disjunct behind the aperture. Aperture ovate, angled above, broadly adnate or slightly disjunct. Inner lip thin, without columellar shelf. Outer lip thin, prosocline, weakly sinuate. Shell anomphalous or with narrowly rimate umbilicus. Periostracum tan.

Operculum (Figure 13C) ovate, amber; nucleus eccentric; dorsal surface very strongly frilled; outer margin sometimes having weak rim. Attachment scar slightly thickened between nucleus and inner edge, whorl edges strongly bulging.

Radula 335 × 60 μm, with 52 rows of teeth. Central tooth 13 μm wide, with highly indented dorsal edge; lateral cusps, 4–6; central cusp narrow, daggerlike; basal cusps medium-sized. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 3-1-4(5); neck medium flexed; outer wing 200% of cutting edge length. Inner marginal teeth with 20–24 cusps; cutting edge occupying 36% of length of tooth. Outer marginal teeth with 23–28 cusps; cutting edge occupying 25% of length of tooth. Stomach slightly longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented or light grey proximally. Snout unpigmented to medium grey-brown. Foot unpigmented or having scattered grey pigment. Opercular lobe medium grey along inner edge, sometimes along sides, unpigmented or diffuse light grey elsewhere. Neck having scattered grey granules to medium grey. Pallial roof and visceral coil medium grey-black, usually lighter on former; gonads often uniform black. Proximal portion of penial filament and distal portion of base darkly pigmented internally.

Ctenidial filaments, 15, without pleats; ctenidium connected to pericardium by medium length efferent vein. Osphradium small, narrow, positioned centrally to slightly posterior to middle of ctenidium. Renal gland longitudinal; kidney opening grey-white. Rectum straight; broadly overlapping genital ducts.

Ovary 0.5 whorl, filling less than 50% of digestive gland behind stomach, abutting posterior edge of stomach. Distal female genitalia shown in Figure 36C. Albumen gland having medium-large (33–45%) pallial component. Capsule gland shorter, narrower than albumen gland, narrowly ovate in section, rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct of two small, overlapping posterior-oblique loops. Oviduct and bursal duct joining at pallial wall. Bursa copulatrix medium length and width, ovate to weakly pyriform, longitudinal, with 50–80% of length posterior to gland. Bursal duct originating from anterior edge at or slightly lateral to mid-line, slightly shorter to slightly longer than bursa, medium width. Seminal receptacle narrow pouchlike, sometimes weakly folded, overlapping anterior portion of bursa.

Testis 1.5 whorls, filling 50% of digestive gland behind stomach, overlapping posterior and part of anterior stomach chamber. Prostate gland small, elongate bean-shaped, pallial portion medium-large (40–50%), narrowly ovate in section. Proximal pallial vas deferens straight. Penis (Figure 36D) small, bladelike; base rectangular, smooth or weakly folded; filament poorly distinguished from base, but apparently medium length and width, tapering to point, longitudinal; lobe absent, distal portion of base gently tapering to filament. Penis lacking glands. Penial duct straight, very close to outer edge.

Type locality: Springs, west-southwest of Hot Springs, Dixie Valley, Pershing County, Nevada, T. 25 N, R. 39 E, SE ¼ section 18 (Figure 52). Holotype, USNM 874391 (Figure 20I), collected by D. W. Sada, 8 September 1991; paratypes, USNM 860688. The type locality is the southernmost spring in a complex of mineralized (1090 micromhos/cm) helocrenes.

Remarks: Among the group of simple-pened species of *Pyrgulopsis,* this species and *P.* ***augustae*** (described below), from nearby Antelope Valley, share a tall shell, weak protoconch microsculpture, short penial filament, and relatively complex coiled oviduct. *Pyrgulopsis* ***dixensis*** differs from *P.* ***augustae*** in its smaller, narrower shell and much weaker frilling of operculum whorls.

Material examined: NEVADA. *Pershing County:* Springs, west-southwest of Hot Springs, USNM 860688, USNM 874391.

Pyrgulopsis ***aurata*** Hershler, sp. nov.

Pleasant Valley pyrg

(Figures 8E, 20K, L, 36E–G)

Etymology: From *auratus* (Latin), golden; referring to endemism of this species in the Goldbanks Hills, Nevada.

Diagnosis: Medium-sized, with ovate-conic shell. Penis medium-sized; filament medium length, lobe short. Penial ornament a small terminal gland.

Description: Shell (Figures 8E, 20K, L) ovate-conic, width/height, 75–83%; height, 2.5–3.0 mm; width, 2.0–2.4 mm; whorls, 4.25–4.75. Protoconch 1.25 whorls, diameter 0.33 mm, weakly wrinkled along edges at apex, otherwise smooth. Teleoconch whorls medium convexity, sutures often impressed, usually shouldered, body whorl often slightly disjunct behind the aperture. Aperture ovate, usually disjunct. Inner lip thick, sometimes having narrow columellar shelf. Outer lip thin, orthocline, weakly sinuate. Umbilicus rimate-perforate. Periostracum tan.

Operculum ovate, amber, nuclear region reddish; nucleus eccentric. Attachment scar slightly thickened between nucleus and inner edge and along inner edge.

Radula 730 × 110 μm, with 60 rows of teeth. Central tooth 24 μm wide, with medium indented dorsal edge; lateral cusps, 4–5; central cusp narrow, daggerlike; basal

cusps medium-sized. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 2(3, 4)-1-3(4); neck medium flexed; outer wing 180% of cutting edge length. Inner marginal teeth with 19–20 cusps; cutting edge occupying 36% of length of tooth. Outer marginal teeth with 23–33 cusps; cutting edge occupying 25% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles light grey or black proximally. Snout unpigmented to medium grey. Foot unpigmented to light grey. Opercular lobe usually black all around, sometimes unpigmented except for black streak along inner edge. Neck unpigmented, except for scattered black granules, to medium grey. Pallial roof, visceral coil often uniformly black, sometimes having lighter pigment on genital ducts. Penial filament darkly pigmented internally.

Ctenidial filaments, 18, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, positioned centrally or slightly posterior to middle of ctenidium. Renal gland longitudinal or slightly oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.75 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 36E. Albumen gland having short pallial component. Capsule gland considerably shorter, as wide or slightly narrower than albumen gland sub-circular in section rectal furrow medium depth. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a posterior-oblique loop (sometimes kinked at mid-line) usually preceded by well-developed posterior twist. Oviduct and bursal duct joining just behind pallial wall. Bursa copulatrix much shorter, narrow, ovate, longitudinal, sometimes overlapped by gland along ventral edge, 25% or less of length posterior to gland. Bursal duct originating from anterior edge at midline, usually poorly distinguished from bursa (which gently tapers anteriorly), slightly longer to twice as long as bursa, narrow-medium width, usually overlapped by albumen gland for 50% of length (distally). Seminal receptacle small, narrow pouchlike, positioned well anterior to bursa copulatrix.

Testis 1.25 whorls, filling more than 50% of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland small, bean-shaped, pallial portion short, ovate in section. Proximal pallial vas deferens with well-developed bend; duct broad. Penis (Figure 36F, G) medium-sized; base elongate-rectangular, inner edge weakly folded; filament a little shorter than base, medium width, tapering to point; lobe shorter than filament, knoblike, longitudinal. Terminal gland small, narrow, transverse, largely or entirely on ventral surface. Penial duct straight, near edge.

Type locality: Coyote Spring, Pleasant Valley, Pershing County, Nevada, T. 30 N, R. 39 E, SE ¼ section 30 (Figure 52). Holotype, USNM 874393 (Figure 20K), collected by D. W. Sada, 7 September 1991; paratypes, USNM 860696. The type locality is a small rheocrene severely impacted by cattle.

Remarks: Among the large group of species having penial ornament solely consisting of a terminal gland, this species closely resembles *P. bryantwalkeri* Hershler, 1994, locally endemic in upper Humboldt basin, in shape of shell and configuration of distal female genitalia. *Pyrgulopsis* ***aurata*** differs in having a nearly smooth protoconch, stronger development of terminal gland (often absent in *P. bryantwalkeri*), narrower bursa copulatrix, and more anteriorly positioned seminal receptacle.

Material examined: NEVADA. *Pershing County:* Coyote Spring, USNM 860696, USNM 874393.

Species from the Lahontan Basin

Pyrgulopsis gibba Hershler, 1995

"Undescribed form of *Fontelicella*" Taylor, 1985:318 [in part; Walker River drainage].

Pyrgulopsis owensensis Hershler, 1989, Hershler & Pratt, 1990:287 [Walker River drainage; not Hershler, 1989].

"Undescribed . . . closely similar [to *P. owensensis*] species" Hershler, 1994:57.

Pyrgulopsis gibba Hershler, 1995:354, 357, 358, figs. 5C, 10–12.

Diagnosis: Medium-sized (rarely small), with ovate- to narrow-conic shell. Penis large; filament medium length, lobe long. Penial ornament a large terminal gland, small Dg3 (sometimes absent), and large ventral gland.

Type locality: Springs west of Fee Reservoir, Surprise Valley, Modoc County, California, T. 46 N, R. 17 E, NE ¼ section 20 (Hershler, 1995:fig. 4C).

Remarks: The distribution of this snail, previously known from Surprise and Duck Lake Valleys in northeastern California, is herein extended into western Nevada to include much of the Lahontan Basin and isolated drainages in the central (Big Smokey, Grass, Smith Creek Valleys) and northwest (Long Valley) parts of the state (Figure 54). The range of this species closely abuts that of widespread *P. kolobensis* and they co-occur in one basin (Crescent Valley), although they are not found in the same springs.

Morphology of this snail is rather uniform throughout its broad range, although populations vary somewhat in size, shell shape, and penial ornament. The terminal gland on the penis may be weakly or strongly fragmented, and in the latter instance is usually accompanied by distal bifurcation of the penial lobe. Development of the ventral gland and Dg3 also varies. Material of this species from the East Walker River drainage was previously treated by the author as disjunct *P. owensensis* (which otherwise is

restricted to the Owens River drainage). Although these species can be confused owing to the general similarity in penial morphology, *P. gibba* is distinguished by various features, including a larger terminal gland on the penis, absence of Dg1, larger seminal receptacle and bursa copulatrix, and pigmented coiled oviduct.

Material examined: CALIFORNIA. *Mono County:* Spring, below Bridgeport Reservoir, East Fork Walker River, T. 6 N, R. 25 E, NW ¼ section 23, USNM 860452. NEVADA. *Elko County:* Spring, Antelope Creek, Humboldt River drainage, T. 37 N, R. 49 E, NE ¼ section 8, USNM 874375, USNM 883987.—Springs, Antelope Creek (upstream from above), Humboldt River drainage, T. 37 N, R. 49 E, SE ¼ section 5, USNM 883988.—Spring, Squaw Creek, Humboldt River drainage, T. 38 N, R. 49 E, SE ¼ section 34, USNM 883986.—Buffalo Springs, Squaw Valley, T. 40 N, R. 47 E, center section 32, USNM 883447. *Eureka County:* Willy Billy Spring, Humboldt River drainage, T. 32 N, R. 51 E, NE ¼ section 32, USNM 874714.—Rattlesnake Spring, Humboldt River drainage, T. 31 N, R. 50 E, NE ¼ section 2, USNM 874812, USNM 883425.—Springs, Pine Creek, Humboldt River drainage (Figure 4F), T. 31 N, R. 52 E, NE ¼ section 7, USNM 858277, USNM 874284.—Willow Spring, Horse Creek Valley, T. 26 N, R. 49 E, NW ¼ section 20, USNM 874310.—Stream, Corral Canyon, Crescent Valley, T. 29 N, R. 47 E, SW ¼ section 32, USNM 874322.—Cold Springs (north), Crescent Valley, T. 31 N, R. 48 E, NE ¼ section 36, USNM 874718. *Humboldt County:* Buck Springs, Black Rock Desert, T. 37 N, R. 24 E, SE ¼ section 23, USNM 874298.—Spring, Tollhouse Canyon, Soldier Meadow drainage, T. 41 N, R. 25 E, section 10, USNM 873201, USNM 873228, USNM 873235.—Buckbrush Springs, Black Rock Desert, T. 38 N, R. 30 E, NE ¼ section 9, USNM 874202, USNM 874894, USNM 883893.—Spring, Bliss Canyon, Black Rock Desert, T. 39 N, R. 31 E, SW ¼ section 6, USNM 874201, USNM 874907.—Springs, near mouth of Jackson Canyon, Black Rock Desert, T. 40 N, R. 31 E, NW ¼ section 28, USNM 874200, USNM 874892.—Springs, Jackson Canyon, Black Rock Desert, T. 40 N, R. 31 E, NE ¼ section 28, USNM 874203, USNM 874906.—Spring, Pueblo Mountains, Alberson Basin, T. 47 N, R. 29 E, NW ¼ section 1, USNM 874214, USNM 874908.—Spring, 0.4 km south of above, Pueblo Mountains, Alberson Basin, T. 47 N, R. 29 E, NW ¼ section 1, USNM 874900.—Craine Creek, Bog Hot Valley, T. 42 N, R. 27 E, NW ¼ section 2, USNM 883924.—Spring, Pearl Canyon, Quinn River Valley, T. 42 N, R. 27 E, center section 25, USNM 883898.—Hillside Spring, Alta Creek Basin, Quinn River Valley, T. 45 N, R. 30 E, NE ¼ section 7, USNM 873429.—Spring, Canyon Creek, Quinn River Valley, T. 45 N, R. 38 E, SW ¼ section 18, USNM 883994.—Spring, 1.6 km northwest of Dyke Hot Springs, Quinn River Valley, T. 42 N, R. 30 E, NW ¼ section 25, USNM 874216, USNM 874743.—Spring, Bishop Canyon, Quinn River Valley, T. 42 N, R. 30 E, SW ¼ section 23, USNM 874210, USNM 874893.—Bonita Spring, Quinn River Valley, T. 37 N, R. 30 E, NE ¼ section 2, USNM 854687.—Trout Creek, Desert Valley, T. 39 N, R. 32 E, NE ¼ section 6, USNM 874217.—Spring, Rock Creek, Humboldt River drainage, T. 34 N, R. 40 E, SW ¼ section 6, USNM 874399.—Spring, Kelly Creek, Humboldt River drainage, T. 40 N, R. 44 E, SW ¼ section 33, USNM 854696.—Spring, Spring Creek, Little Humboldt River drainage, T. 41 N, R. 43 E, NE ¼ section 23, USNM 883922.—Layton Spring, South Fork Little Humboldt River, T. 41 N, R. 43 E, SE ¼ section 11, USNM 883897, USNM 883923. *Lander County:* Twin Spring, Grass Valley, T. 22 N, R. 47 E, SE ¼ section 12, USNM 874300.—Stream, Potato Canyon, Grass Valley, T. 23 N, R. 48 E, NE ¼ section 9, USNM 874329.—Spring, Fish Creek, Reese River Valley, T. 27 N, R. 42 E, center section 16, USNM 883849.—Spring, southwest of Bradley Spring, Reese River Valley, T. 22 N, R. 43 E, NE ¼ section 28, USNM 874400.—Twin Springs, Smith Creek Valley, T. 18 N, R. 39 E, NW ¼ section 27, USNM 874407. *Lyon County:* Spring, (lower) Dalzell Canyon, Smith Valley, T. 8 N, R. 25 E, NW ¼ section 5, USNM 860453, USNM 874394.—Spring, (upper) Dalzell Canyon, Smith Valley, T. 9 N, R. 24 E, SW ¼ section 24, USNM 873352, USNM 874398.—Spring, Nye Canyon, Smith Valley, T. 8 N, R. 25 E, NE ¼ section 9, USNM 883544. *Nye County:* Spring, Indian Creek, Reese River Valley, T. 11 N, R. 40 E, NW ¼ section 4, USNM 874379, USNM 874395.—Springs, RO Ranch, Big Smokey Valley, T. 13 N, R. 44 E, NE ¼ section 32, USNM 874405. *Pershing County:* Buffalo Springs, Buena Vista Valley, T. 27 N, R. 35 E, west ½ section 2, USNM 874752, USNM 883449.—Spring, 1.6 km west of Fitting, Buena Vista Valley, T. 29 N, R. 34 E, S ½ section 35, USNM 874747.—Spring, Spring Valley, T. 28 N, R. 34 E, NW ¼ section 3, USNM 874751, USNM 883482.—Dago Spring, Buena Vista Valley, T. 27 N, R. 37 E, NW ¼ section 16, USNM 874737.—Buena Vista Creek, Buena Vista Valley, T. 30 N, R. 34 E, NE ¼ section 28, USNM 883453.—Kitten Spring, Buena Vista Valley, T. 25 N, R. 36 E, NW ¼ section 10, USNM 874750.—Twin Springs, Buena Vista Valley, T. 27 N, R. 37 E, SW ¼ section 29, USNM 874748.—Porter Spring, Granite Springs Valley, T. 29 N, R. 28 E, NW ¼ section 5, USNM 883446.—Spring, 0.4 km east of Porter Spring, Granite Springs Valley, T. 29 N, R. 28 E, NE ¼ section 5, USNM 874749, USNM 883433.—Spring (pond outflow), Sheep Ranch Canyon, Grass Valley, T. 32 N, R. 39 E, NW ¼ section 16, USNM 874746.—Spring, Clearwater Creek, Grass Valley, T. 33 N, R. 38 E, SW ¼ section 13, USNM 874755, USNM 883440.—Spring, Sacramento Canyon, Humboldt River drainage, T. 29 N, R. 33 E, NE ¼ section 35, USNM 874742.—Spring, Pleasant Valley Ranch, Pleasant Valley, T. 27 N, R. 38 E, NE

¼ section 2, USNM 874389. *Washoe County:* Spring, Hog Gulch, Surprise Valley, T. 42 N, R. 18 E, SE ¼ section 10, USNM 883989.—North Spring, Surprise Valley, T. 42 N, R. 18 E, NW ¼ section 11, USNM 883992.—Small Spring, Surprise Valley, T. 41 N, R. 18 E, NW ¼ section 28, USNM 883990.—Spring, 3.2 km south of Mosquito Lake, Mosquito Valley, T. 45 N, R. 19 E, SE ¼ section 22, USNM 874204, USNM 874897.—Spring, west of Alkali Lake, Long Valley, T. 44 N, R. 19 E, NW ¼ section 32, USNM 874205.—Spring, Vya, Long Valley, T. 42 N, R. 19 E, SW ¼ section 4, USNM 874898.—Spring, 3.2 km northeast of Middle Lake, Long Valley, T. 45 N, R. 21 E, SW ¼ section 30, USNM 874895.—Spring, Wall Creek, 1.6 km above reservoir, Duck Flat drainage, T. 38 N, R. 19 E, SE ¼ section 12, USNM 874287, USNM 883926.—Spring, Wall Creek, 4.8 km above reservoir, Duck Flat drainage, T. 38 N, R. 20 E, NE ¼ section 6, USNM 874268, USNM 883925.—"Deep Hole Spring" (="Big Hole Spring"), 14.4 km west-northwest of Gerlach, Smoke Creek Desert, T. 33 N, R. 22 E, NW ¼ section 27, USNM 873230, USNM 874272.—Spring, Red Mountain Creek, Hualapai Flat, T. 35 N, R. 22 E, SW ¼ section 15, USNM 874198, USNM 874905.—Spring, Red Mountain Creek, Hualapai Flat, T. 35 N, R. 22 E, SW ¼ section 14, USNM 874890. OREGON. *Lake County:* Foskett Spring, Coleman Valley, T. 40 S, R. 24 E, NW ¼ section 25, USNM 883545, USNM 892031.—Moss Spring, Chewaucan River drainage, T. 36 S, R. 19 E, SE ¼ section 5, USNM 883543.

Pyrgulopsis wongi Hershler, 1989

Pyrgulopsis wongi Hershler, 1989:196, figs. 41–47.

Diagnosis: Small to medium-sized, with globose to low-conical shell. Penis large; filament and lobe medium length. Penial ornament a large terminal gland, large penial gland, large, fused Dg1–2; medium-sized Dg3, two to five additional dorsal glands; and two medium-sized ventral glands.

Type locality: Spring, Birchim Canyon, Owens Valley, Inyo County, California, T. 6 S, R. 31 E, SE ¼ section 9.

Remarks: The range of this species, previously constituting the pluvial Owens River drainage and adjacent basins (Deep Springs, Fish Lake, and Huntoon Valleys), is herein extended to a portion of the eastern Lahontan Basin (upper portions of the Carson and East Walker River drainages), and a nearby, isolated drainage (Teels Marsh) (Figure 52). This snail does not exhibit marked variation in shell or anatomical features.

Material examined: CALIFORNIA. *Mono County:* Spring, Clark Canyon, East Walker River drainage, T. 4 N, R. 25 E, SE ¼ section 1, USNM 874191.—Spring, Clearwater Creek, East Walker River drainage, T. 4 N, R. 26 E, NW ¼ section 28, USNM 874193.—Spring, Rough Creek, East Walker River drainage, T. 5 N, R. 27 E, SE ¼ section 7, USNM 874188. NEVADA. *Douglas County:* Doud Springs, Carson River drainage, T. 11 N, R. 21 E, SE ¼ section 20, USNM 874741. *Esmeralda County:* Spring, southwest of The Crossing, Fish Lake Valley, T. 1 S, R. 36 E, SW ¼ section 17, USNM 883983.—Spring, southwest of The Crossing, 75 m west of above, Fish Lake Valley, T. 1 S, R. 36 E, SW ¼ section 17, USNM 883982. *Mineral County:* Spring, Bodie Creek, East Walker River drainage, T. 6 N, R. 27 E, SE ¼ section 25, USNM 874404.—Jacks Spring, Teels Marsh drainage, T. 2 N, R. 31 E, NE ¼ section 2, USNM 874763, USNM 874880.

Pyrgulopsis ***longiglans,*** Hershler, sp. nov.

Western Lahontan pyrg

(Figures 8F, 20M–P, 37A–C)

Etymology: From *glans* (Latin), gland; and *longus,* long; referring to the elongate penial gland characterizing this species.

Diagnosis: Small to medium-sized, with sub-globose to ovate-conic shell. Penis large; filament and lobe medium length. Penial ornament a large terminal gland, large penial gland, small Dg1, small Dg2, and large ventral gland (sometimes reduced or absent).

Description: Shell (Figures 8F, 20M–P) sub-globose to ovate-conic, width/height, 67–88%; height, 1.4–2.6 mm; width, 1.1–1.9 mm; whorls, 3.75–4.5. Protoconch 1.25–1.3 whorls, diameter 0.29 mm, initial 0.75 whorl weakly wrinkled along inner edge, otherwise smooth. Teleoconch whorls medium convexity; shoulders well developed, sutural shelf often broad. Aperture ovate, adnate or slightly disjunct. Inner lip slightly thickened, without columellar shelf. Outer lip thin, orthocline-slightly prosocline, without sinuation. Umbilicus rimate-shallowly perforate. Periostracum tan.

Operculum ovate, reddish; nucleus eccentric; dorsal surface smooth or weakly frilled. Attachment scar slightly thickened between nucleus and inner edge, and along outer edge.

Radula 1.05 mm × 140 μm, with 63 rows of teeth. Central tooth 23 μm wide, with medium indented dorsal edge; lateral cusps, 3–5; central cusp medium width, daggerlike; basal cusps medium-sized. Basal process V-shaped, basal sockets deep. Lateral tooth formula 2(3)-1-3; neck weakly flexed; outer wing 175% of cutting edge length. Inner marginal teeth with 18–22 cusps (basal cusp enlarged); cutting edge occupying 36% of length of tooth. Outer marginal teeth with 28–32 cusps; cutting edge occupying 27% of length of tooth. Stomach slightly longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum very small.

Cephalic tentacles having small black patch of internal

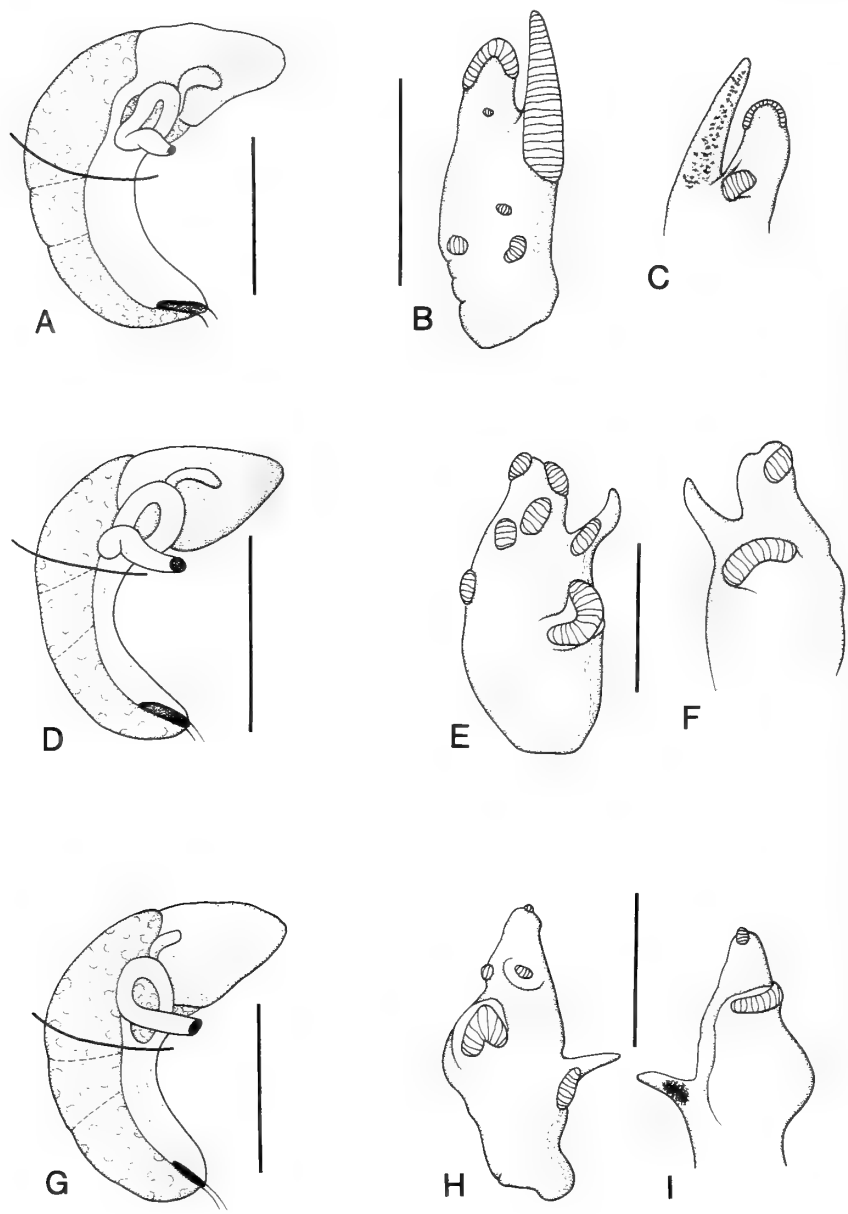


Figure 37

Genitalia of *Pyrgulopsis* species (A, *P.* ***longiglans,*** USNM 860701; B, C, *P.* ***longiglans,*** USNM 874745; D–F, *P.* ***militaris,*** USNM 860704; G–I, *P.* ***umbilicata,*** USNM 860705). A. Bar = 0.5 mm. B, C. Bar = 1.0 mm. D-I. Bars = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures (viewed from left side), dorsal aspect of penis, ventral aspect of distal penis.

pigment proximally; distal section unpigmented except for central light grey band or uniformly light grey. Snout medium grey to black. Foot light to medium grey or black. Opercular lobe black along inner edge and sides; light to medium grey elsewhere. Neck light to medium grey. Pallial roof, visceral coil uniform black. Ventral penial filament pigmented with scattered black granules.

Ctenidial filaments, 13, weakly pleated, ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, positioned alongside posterior half of ctenidium. Renal gland longitudinal; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.75–1.0 whorl, filling 50% of digestive gland behind stomach, slightly overlapping posterior stomach chamber. Distal female genitalia shown in Figure 37A. Albumen gland having short pallial component. Capsule

gland as wide, as long or slightly longer than albumen gland; sub-circular in section; rectal furrow weak. Ventral channel broadly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a posterior oblique loop, often kinked in mid-line, preceded by small posterior twist. Oviduct and bursal duct joining well behind pallial wall; common duct broad. Bursa copulatrix as wide and 67% as long as albumen gland, pyriform, with blunt anterior edge, longitudinal, entire length posterior to gland. Bursal duct originating from anterior edge at mid-line, short, medium width, but broadening distally. Seminal receptacle small, pouchlike, overlapping anterior half of bursa, positioned posterior to albumen gland.

Testis 1.0 whorl, filling 50% of digestive gland behind stomach, slightly overlapping posterior stomach chamber. Prostate gland bean-shaped, pallial portion medium, narrowly ovate in section. Proximal pallial vas deferens having well-developed, reflexed loop. Penis (Figure 37B, C) large; base rectangular, sometimes folded along inner edge; filament slightly shorter than base, medium width, tapering to a pointed tip, longitudinal; lobe medium length, knoblike, longitudinal. Terminal gland large, medium width, curved, transverse, extending onto both dorsal and ventral surfaces. Penial gland usually filling entire length and width of filament, slightly overlapping base. Dg1 small, usually transverse (sometimes circular or oblique), positioned well proximal to penial gland near outer edge. Dg2 small, similar to Dg1 in appearance, sometimes weakly raised, positioned proximally near or along inner edge. Dotlike glands sometimes present near center of lobe (vestige of Dg3?) and just distal to Dg1. Ventral gland large (reduced or absent in some populations), sub-circular, borne on weak swelling, ransverse or oblique, positioned near base of filament. Penial duct straight, near outer edge.

Type locality: Spring, north-northwest of Holbrook Junction, Antelope Valley, Douglas County, Nevada, T. 10 N, R. 22 E, SW ¼ section 6. Holotype, USNM 873409 (Figure 20M), collected by D. W. Sada, 1 July 1989; paratypes, USNM 860701. The type locality is a small rheocrene impounded several meters below the source.

Remarks: A full complement of glands on the penis, including an enlarged penial gland, is found in several other congeners in the region, notably *P. **fausta,*** but also *P. californiensis* (Gregg & Taylor, 1965) and *P. wongi. Pyrgulopsis **longiglans*** differs from these species in having weakly developed Dg2 and Dg3, and a smaller ventral gland. This species is distributed in the western portion of the Lahontan Basin as well as in adjacent Antelope Valley (Figure 52).

Material examined: NEVADA. *Douglas County:* Spring, north-northwest of Holbrook Junction, USNM 873409, USNM 874745.—Spring, 2.4 km south of Double Spring, Antelope Valley, T. 11 N, R. 21 E, SW ¼ section 36, USNM 874396, USNM 874753. *Humboldt County:* Spring, 11.3 km west of Double Hot Spring, Black Rock Desert, T. 36 N, R. 25 E, NW ¼ section 5, USNM 874292, USNM 883445.—Spring, 2.3 km west of Wagner Spring, Black Rock Desert, T. 37 N, R. 25 E, NE ¼ section 6, USNM 874295.—Spring, 2.4 km west of Wagner Spring, Black Rock Desert, T. 37 N, R. 25 E, NE ¼ section 6, USNM 874299, USNM 883451.—Spring, 3.2 km west of Bronco Spring, Black Rock Desert, T. 37 N, R. 25 E, NW ¼ section 21, USNM 874297, USNM 883846.—Spring, Jackass Flat, Black Rock Desert, T. 37 N, R. 25 E, NE ¼ section 21, USNM 874288.—Spring, Paiute Creek, Black Rock Desert, T. 40 N, R. 26 E, NW ¼ section 28, USNM 874270.—Spring, Little Smokey Creek, south of road, Black Rock Desert, T. 38 N, R. 23.5 E, NW ¼ section 24, USNM 874223.—Spring, Little Smokey Creek, east of road, Black Rock Desert, T. 38 N, R. 23.5 E, NW ¼ section 24, USNM 874197.—Spring, Little Smokey Creek, north of road, Black Rock Desert, T. 38 N, R. 23.5 E, NW ¼ section 24, USNM 874221.—Spring, Little Smokey Creek, Black Rock Desert, T. 38 N, R. 23.5 E, section 24, USNM 892024.—Spring, Calico Hills, Black Rock Desert, USNM 873223. *Washoe County:* Spring, Hardscrabble Creek, Pyramid Lake Basin, T. 24 N, R. 21 E, SE ¼ section 19, USNM 858276.—Sevenmile Spring, Winnemucca Lake Basin, T. 25 N, R. 23 E, NE ¼ section 9, USNM 874891, USNM 883436.—Spring, southeast of Nugent Springs, Winnemucca Lake Basin, T. 26 N, R. 23 E, SE ¼ section 10, USNM 874904.—Wildcat Spring, North Fork Buffalo Creek, Smoke Creek Desert, T. 34 N, R. 19 E, SW ¼ section 26, USNM 874293.

*Pyrgulopsis **militaris,*** Hershler, sp. nov.

Northern Soldier Meadow pyrg

(Figures 8G, 15G–I, 21A, B, 37D–F)

Etymology: From *militaris* (Latin), of soldiers and war; referring to occurrence of this species in Soldier Meadows, which was named after a U.S. Army camp stationed in the area during the 1860s (Garside & Schilling, 1979: 38).

Diagnosis: Small, with sub-globose to ovate-conic shell. Penis large; filament short, lobe medium length. Penial ornament a small terminal gland, small penial gland, large Dg1, small Dg2, small Dg3, 1-2 additional dorsal glands, and medium-sized ventral gland.

Description: Shell (Figures 8G, 21A, B) sub-globose to ovate-conic, width/height, 75–92%; height, 1.2–1.9 mm; width, 1.1–1.5 mm; whorls, 3.75–4.25. Protoconch 1.25 whorls, diameter 0.24 mm, surface finely wrinkled (sculpture weakening on later portion, which sometimes has weak spiral elements), sculpture on initial 0.75 whorl

sometimes further developed as pits. Teleoconch whorls medium convexity, shouldered, sometimes having strong sub-sutural angulation on body whorl; body whorl often slightly disjunct behind the aperture in larger specimens. Aperture ovate, angled above; adnate or, more commonly, slightly disjunct. Inner lip sometimes slightly thickened, without columellar shelf. Outer lip thin, orthocline-prosocline, without sinuation. Umbilicus perforate; umbilical region sometimes narrowly excavated. Periostracum tan.

Operculum ovate, amber; nucleus eccentric; dorsal surface frilled. Attachment scar slightly thickened between nucleus and inner edge and sometimes along portions of outer and/or inner edges.

Radula (Figure 15G–I) 890 × 140 μm, with 64 rows of teeth. Central tooth 18 μm wide, with highly indented dorsal edge; lateral cusps, 5–6; central cusp long and narrow, daggerlike; basal cusps small. Basal tongue broad U-shaped, basal sockets medium depth. Lateral tooth formula 2(3)-1-3(4); neck weakly flexed; outer wing 190% of cutting edge length. Inner marginal teeth with 23–27 cusps; cutting edge occupying 34% of length of tooth. Outer marginal teeth with 25–30 cusps; cutting edge occupying 26% of length of tooth. Stomach slightly longer than style sac; stomach chambers equal-sized; stomach caecum very small.

Cephalic tentacles unpigmented to medium brown. Snout medium to dark brown or black. Foot, neck light to dark brown. Opercular lobe dark along inner edge, remaining portion medium brown. Pallial roof, visceral coil uniform dark brown or black. Penial filament darkly pigmented internally.

Ctenidial filaments, 15, without pleats, ctenidium overlapping pericardium posteriorly. Osphradium small, narrowly ovate, centered slightly posterior to middle of ctenidium. Renal gland slightly oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.5–0.75 whorl, filling more than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 37D. Albumen gland having very short or no pallial component. Capsule gland longer and slightly narrower or as wide as albumen gland, sub-circular in section; rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a posterior-oblique loop preceded by prominent posterior twist. Oviduct and bursal duct joining well behind pallial wall. Bursa copulatrix as long and wide as albumen gland, ovate-pyriform, longitudinal, most of length posterior to gland. Bursal duct originating from anterior edge lateral to mid-line, very short, medium width. Seminal receptacle small, narrow, pouchlike, overlapping middle of bursa.

Testis 1.25 whorls, filling more than 50% of digestive gland behind stomach, overlapping posterior and part of anterior stomach chamber. Prostate gland bean-shaped, pallial portion short, ovate in section. Proximal pallial vas deferens with well-developed, reflexed loop; duct broad. Penis (Figure 37E, F) large; base rectangular, weakly folded or smooth; filament short, narrow, tapering to point, longitudinal or slightly oblique; lobe a little longer than filament, knoblike, longitudinal. Terminal gland small, narrow, rarely divided into two units, curving, transverse, largely on ventral surface. Penial gland usually filling proximal half of filament (rarely filling entire length), slightly narrower than filament. Dg1 large, borne on prominent swelling, sometimes slightly curved, longitudinal, positioned slightly behind filament. Dg2 small, sub-circular, positioned along inner edge medially. Dg3 small, ovate, positioned along outer edge of lobe. Base rarely bearing small, dotlike gland alongside Dg2 distally. Dorsal surface of lobe also bearing one to two small glands. Ventral gland medium-sized, narrow, borne on prominent pedicel, transverse, positioned near centrally. Penial duct straight, near outer edge.

Type locality: Spring, west of Soldier Meadow Ranch, Black Rock Desert drainage, Humboldt County, Nevada, T. 40 N, R. 25 E, SW ¼ section 5. Holotype, USNM 873203 (Figure 21A), collected by J. Jerry Landye, 3 June 1978; paratypes, USNM 860704. The type locality is a small, thermal (30°C.) rheocrene that is impounded downstream. This site is Spring Number 2 of Nyquist (1963). Note that the second locality for this species, West Spring in nearby Craine Creek drainage, was only mildly thermal (23°C).

Remarks: This snail and the three species locally endemic in Soldier and Mud Meadows drainage compose a well-defined group of *Pyrgulopsis* having a full complement of penial glands, simply coiled oviduct, large bursa copulatrix positioned entirely posterior to the albumen gland, and a small, narrow seminal receptacle. Members of this group also have small, squat shells with weak protoconch sculpture; long, narrow central cusps on the central radular teeth; short penial filament; well-developed, tapered penial lobe; weakly developed terminal gland, and small-medium penial gland. Among the species of this group, *P. **militaris*** resembles *P. **limaria*** (described below) in that the penis is endowed with a well-developed penial gland, Dg1, and ventral gland. *Pyrgulopsis **militaris*** differs from *P. **limaria*** in that the penis lacks a distal swelling along the inner edge, has a weaker Dg2; and the distal female oviduct is more complexly coiled. The distribution of this species is shown in Figure 52.

Material examined: NEVADA. *Humboldt County:* Spring, west of Soldier Meadow Ranch, USNM 860704, USNM 873203, USNM 883991, USNM 892043.—West Spring, Craine Creek drainage, T. 44 N, R. 27 E, NW ¼ section 20, USNM 873156, USNM 883921.

Pyrgulopsis ***umbilicata*** Hershler, sp. nov.

Southern Soldier Meadow pyrg

(Figures 8H, 21C, D, 37G–I)

Etymology: From *umbilicatus* (Latin), navel; referring to the prominent umbilicus in shells of this species.

Diagnosis: Small to medium-sized, with sub-globose to ovate-conic shell. Penis large, filament short, lobe long. Penial ornament a small terminal gland, medium-sized Dg1, large Dg2, small Dg3, and medium-sized ventral gland.

Description: Shell (Figures 8H, 21C, D) sub-globose to ovate-conic, width/height, 78–90%; height, 1.7–2.4 mm; width, 1.4–1.9 mm; whorls, 4.0–4.5. Protoconch 1.3 whorls, diameter 0.26 mm, surface usually partly eroded, appearing nearby smooth. Teleoconch whorls highly convex; shoulders weak or absent. Aperture ovate, narrowly adnate. Inner lip thin or slightly thickened, without columellar shelf. Outer lip thin, orthocline, without sinuation. Umbilicus perforate; umbilical region sometimes narrowly excavated. Periostracum tan.

Operculum ovate, amber; nucleus eccentric; dorsal surface frilled. Attachment scar thick all around.

Radula 1.29 mm × 163 μm, with 72 rows of teeth. Central tooth 18 μm wide, with medium indented dorsal edge; lateral cusps, 4–5; central cusp narrow, daggerlike, basal cusps small, sometimes accompanied by slight thickening to the inside. Basal tongue broad U-shaped, basal sockets medium depth. Lateral tooth formula 2(3)-1-3(4); neck weakly flexed, outer wing 170% of cutting edge length. Inner marginal teeth with 21–25 cusps; cutting edge occupying 32% of length of tooth. Outer marginal teeth with 26–28 cusps; cutting edge occupying 25% of length of tooth. Stomach slightly longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles light to dark grey-brown. Snout medium brown. Foot, neck medium to dark grey-brown. Opercular lobe black along inner edge, otherwise medium brown. Pallial roof, visceral coil uniformly dark brown-black. Ventral surface of penial filament darkly pigmented along proximal half.

Ctenidial filaments, 16, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrowly ovate, centered slightly posterior to middle of ctenidium. Renal gland oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.75–1.0 whorl, filling 50% of digestive gland behind stomach. Distal female genitalia shown in Figure 37G. Capsule gland slightly shorter to slightly longer, slightly narrower than albumen gland, sub-circular in section; rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a circular to posterior-oblique loop, preceded by weak twist, or weakly kinked at mid-length. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copulatrix as long and wide as albumen gland, sub-globose to broadly pyriform, longitudinal, most of length posterior to gland. Bursal duct originating from anterior edge at mid-line, very short, narrow to medium width. Seminal receptacle very small, narrow pouchlike, overlapping anterior or middle portion of bursa.

Testis 1.25 whorls, filling more than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Prostate gland fat bean-shaped, pallial portion short, ovate in section. Proximal pallial vas deferens having well-developed, reflexed loop; duct broad. Penis (Figure 37H, I) large; base near square to rectangular, swollen along inner edge distally, weakly folded; filament short, narrow, tapering to point, oblique; lobe often longer than base, tapering, longitudinal. Terminal gland small, narrow-circular, rarely divided into two units, sometimes longitudinal, most of length on ventral surface. Dg1 positioned distally, overlapping as much as proximal half of filament, as wide as filament. Dg2 large, borne on pronounced swelling, sometimes curved (fused?), or accompanied by additional glandular unit (and rarely a second dotlike unit) to outer side, positioned along inner edge distally. Dg3 small, rarely absent, weakly raised, positioned near middle of lobe. Ventral gland medium-sized, narrow, borne on prominent swelling, transverse, positioned on ventral surface of lobe, usually curving onto inner edge of dorsal surface, rarely accompanied by dotlike unit medially. Penial duct straight, near outer edge.

Type locality: Spring, near mouth of Warm Springs Canyon, Soldier Meadow, Humboldt County, Nevada, T. 40 N, R. 25 E, NW ¼ section 18. Holotype, USNM 873208 (Figure 21C), collected by J. Jerry Landye, 3 June 1978; paratypes, USNM 860705. The type locality is a small, thermal (36–37°C.) rheocrene. This site is Spring Number 6 of Nyquist (1963).

Remarks: This snail resembles *P.* ***limaria*** (described below) in having a rather long, tapered penial lobe, and highly reduced terminal gland, but differs from this and other species in the Soldier Meadows area in that Dg1 overlaps the penial filament. The distribution of this species is shown in Figure 52.

Material examined: NEVADA. *Humboldt County:* Spring, near mouth of Warm Springs Canyon, Soldier Meadow, USNM 860705, USNM 873208, USNM 892044.—Spring, south of above (Spring Number 5 of Nyquist [1963]), Soldier Meadow, T. 40 N, R. 25 E, NW ¼ section 18, USNM 873202, USNM 874922.—Spring, south of Big Hole, Soldier Meadow, T. 40 N, R. 25 E, NW ¼ section 18, USNM 874296, USNM 874896.

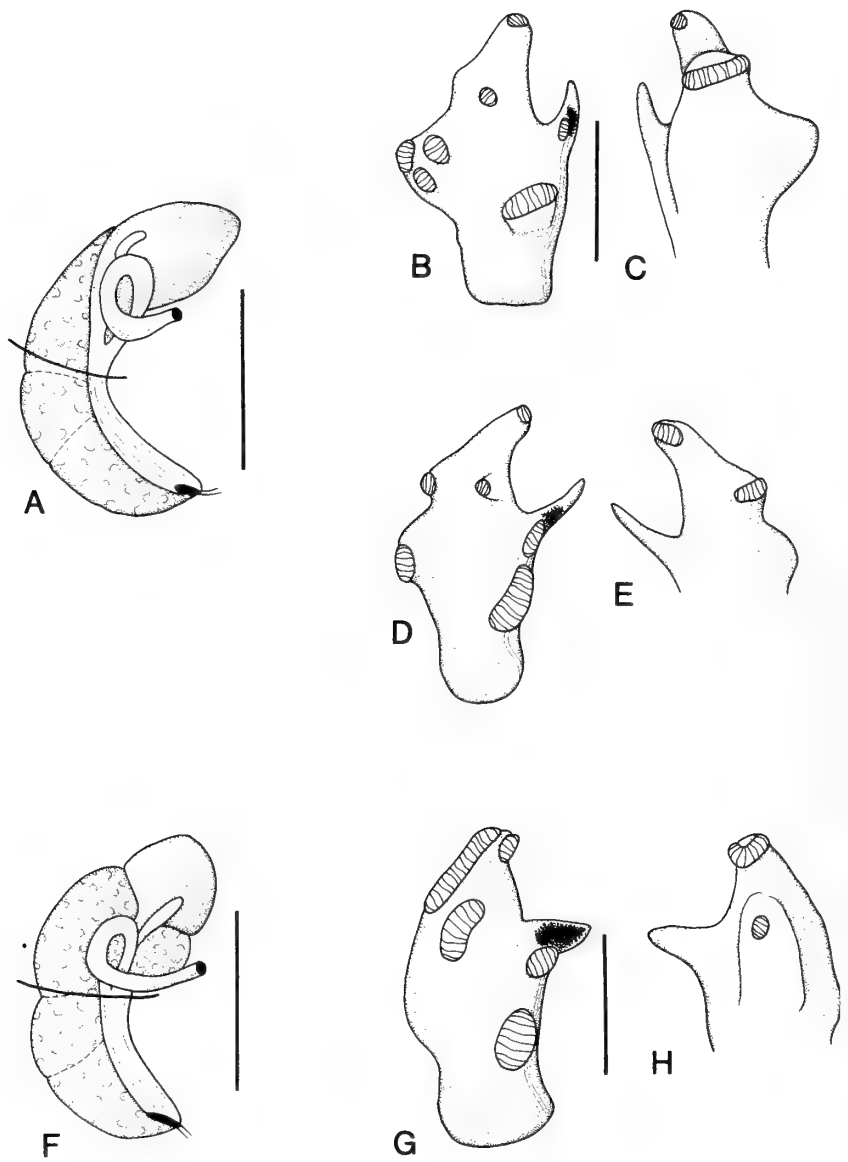


Figure 38

Genitalia of *Pyrgulopsis* species (A–E, *P. **limaria,*** USNM 860706; F–H, *P. **notidicola,*** USNM 860707). Bars = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis. Two sets of penes (B, C; D, E) are shown for *P. **limaria.***

*Pyrgulopsis **limaria*** Hershler, sp. nov.

Squat Mud Meadows pyrg

(Figures 8I, 21E–F, 38A–E)

Etymology: From *limarius* (Latin), of mud; referring to endemism of this species in Mud Meadows drainage, Nevada.

Diagnosis: Small, with low trochoid to ovate-conic shell. Penis large, filament short, lobe medium length. Penial ornament a small terminal gland, small penial gland, large Dg1; small Dg2, sometimes accompanied by one to two similarly sized glands to outer side; small Dg3, and medium-large ventral gland.

Description: Shell (Figures 8I, 21E, F) low trochoid to ovate-conic, width/height, 86–101%; height, 1.3–1.7 mm; width, 1.3–1.6 mm; whorls, 3.75–4.25. Protoconch 1.25 whorls, diameter 0.28 mm, initial 0.75 whorl finely wrinkled (partly eroded), otherwise near smooth. Teleoconch whorls highly convex, strongly shouldered. Aperture

ovate, narrowly adnate or slightly disjunct. Inner lip thin, without columellar shelf. Outer lip thin, orthocline, without sinuation. Umbilicus deeply perforate. Periostracum tan.

Operculum ovate, dark amber; nucleus eccentric; dorsal surface smooth; outer margin sometimes having very weak rim. Attachment scar slightly thickened between nucleus and inner edge and along inner edge.

Radula 1.15 mm × 150 μm, with 62 rows of teeth. Central tooth 19–24 μm wide, with medium indented dorsal edge; lateral cusps, 4–5; central cusp long, narrow, dagger-like; basal cusps small, sometimes accompanied by weak thickenings on inner sides. Basal tongue broad V-shaped, basal sockets medium depth. Lateral tooth formula 2(3)-1-3(4); neck very weakly flexed (nearly straight); outer wing 175% of cutting edge length. Inner marginal teeth with 19–21 cusps; cutting edge occupying 30% of length of tooth, near basal cusp enlarged. Outer marginal teeth with 25–30 cusps; cutting edge occupying 26% of length of tooth. Stomach slightly longer than style sac; stomach chambers equal-sized; stomach caecum small.

Cephalic tentacles unpigmented or having light brown patch just proximal to eyes. Snout light to medium brown. Foot unpigmented or very light brown. Opercular lobe dark along inner edge, sometimes along sides. Neck unpigmented except for scattered internal granules. Pallial roof, visceral coil near uniform dark brown. Penial filament darkly pigmented along proximal half.

Ctenidial filaments, 14, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrowly ovate, centrally positioned. Renal gland longitudinal; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.5–0.75 whorl, filling 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 38A. Albumen gland having very short or no pallial component. Capsule gland longer and as wide as albumen gland, sub-circular in section; rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a U-shaped or open, posterior-oblique loop. Oviduct and bursal duct joining well behind pallial wall. Bursa copulatrix as long and wide as albumen gland, ovate-pyriform, longitudinal, most of length posterior to gland. Bursal duct originating from anterior edge at or lateral to mid-line, very short, medium width. Seminal receptacle very small, narrow pouchlike, overlapping anterior portion or middle of bursa.

Testis 1.0–1.25 whorls, filling more than 50% of digestive gland behind stomach, overlapping posterior and part of anterior stomach chamber anteriorly. Prostate gland ovate, pallial portion short, ovate in section. Proximal pallial vas deferens having well-developed, often slightly recflexed loop. Penis (Figure 38B–E) large; base rectangular, swollen along inner edge distally; filament short, narrow, tapering to point, longitudinal or slightly oblique; lobe medium length, clublike, narrowed distally, longitudinal. Terminal gland small, circular or narrow-longitudinal, rarely divided, overlapping ventral slightly more than dorsal surface. Penial gland usually filling less than 50% of filament length, as wide or slightly narrower than filament, sometimes extending slightly onto base, occasionally abutting or fused with Dg1. Dg1 large, borne on pronounced swelling, longitudinal or slightly curving across base, positioned slightly to considerably proximal to filament. Dg2 small, sometimes curved (fused with above?), positioned along inner edge medially, often accompanied by one to two smaller glands on outer side. Dg3 small or dotlike, often borne on raised swelling, positioned near middle of lobe, often accompanied by additional, similarly sized gland. Ventral gland medium-large, rarely divided, borne on prominent swelling, transverse, positioned on basal portion of lobe, sometimes extending onto inner edge of dorsal surface. Penial duct straight, near outer edge.

Type locality: Spring brook, Mud Meadow drainage, Humboldt County, Nevada, T. 40 N, R. 24 E, NE ¼ section 26. Holotype, USNM 873232 (Figure 21E), collected by J. Jerry Landye, 30 August 1979; paratypes, USNM 860706. The type locality is a thermal (32°C) spring brook modified to form a drainage ditch. This species also was present at the thermal spring source (ca. 400 m upflow; 34°C).

Remarks: This snail differs from other species in the Soldier Meadows area in having a pronounced swelling along inner edge of penis distally and frequently having small glands adjacent to Dg2.

Material examined: NEVADA. *Humboldt County:* Spring brook, Mud Meadow drainage, USNM 860706, USNM 873232, USNM 892045.—Spring brook, 1 km upflow from above, Mud Meadow drainage, T. 40 N, R. 24 E, NE ¼ section 26, USNM 892047.—Spring, Mud Meadow drainage, T. 40 N, R. 24 E, NE ¼ section 23, USNM 874291.

Pyrgulopsis ***notidicola*** Hershler, sp. nov.

Elongate Mud Meadows pyrg

(Figures 8J, 21G, H, 38F–H)

Etymology: From *notis* (Greek), wetness, and *-colus* (Latin), dwelling in; referring to the amphibious habit of this species.

Diagnosis: Small to medium-sized, with ovate- to narrow-conic shell. Penis large; filament short, lobe medium length. Penial ornament a large terminal gland, medium-sized penial gland, large Dg1, additional dorsal gland on lobe (not corresponding to either Dg2 or Dg3), and very small ventral gland.

Description: Shell (Figures 8J, 21G, H) ovate- to narrow-conic, width/height; 76–96%; height, 1.3–2.4 mm; width, 1.2–1.9 mm; whorls, 3.5–4.25. Protoconch 1.3 whorls, diameter 0.29 mm, initial 0.75 whorl finely wrinkled, otherwise smooth. Teleoconch whorls highly convex, shoulders well developed; body whorl often slightly disjunct behind the aperture. Aperture ovate, usually slightly disjunct. Inner lip slightly thickened, sometimes having narrow columellar shelf. Outer lip thin, prosocline, without sinuation. Umbilicus rimate, sometimes nearly absent; umbilical region sometimes narrowly excavated. Periostracum tan.

Operculum ovate; nucleus eccentric; dorsal surface very weakly frilled; outer margin sometimes having very weak rim. Attachment scar slightly thickened between nucleus and inner edge and along inner edge.

Radula 1.52 mm × 156 μm, with 75 rows of teeth. Central tooth 25–28 μm wide, with medium indented dorsal edge; lateral cusps, 4–6; central cusp long, narrow, daggerlike; basal cusps medium-sized, sometimes accompanied by weak swelling to inner sides. Basal tongue broad V-shaped, basal sockets medium depth. Lateral tooth formula 2(3, 4)-1-4(5); neck very weakly flexed or straight; outer wing 160% of cutting edge length. Inner marginal teeth with 23–26 cusps, basal cusps enlarged; cutting edge occupying 33% of length of tooth. Outer marginal teeth with 22–27 cusps; cutting edge occupying 26% of length of tooth. Stomach slightly longer than style sac; anterior stomach chamber slightly larger than posterior chamber; stomach caecum very small.

Cephalic tentacles light brown. Snout, foot, light to medium brown. Opercular lobe dark along inner edge, pigment slightly lighter elsewhere. Neck unpigmented or light brown. Pallial roof, visceral coil uniform dark brown-black. Penial filament darkly pigmented internally.

Ctenidial filaments, 17, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrowly ovate, centered slightly posterior to middle of ctenidium. Renal gland strongly oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.5 whorl, filling less than 50% of digestive gland behind stomach, abutting posterior edge of stomach. Distal female genitalia shown in Figure 38F. Albumen gland without pallial component. Capsule gland longer and slightly narrower to as wide as albumen gland, sub-circular in section; rectal furrow moderately developed. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a circular or posterior-oblique loop. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix slightly narrower than albumen gland, medium length, globular, longitudinal, most of length posterior to gland. Bursal duct originating from anterior edge at mid-line, slightly shorter than bursa, narrow-medium width. Seminal receptacle small, narrow, digitate, overlapping anterior or middle of bursa.

Testis 0.75–1.0 whorl, filling 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Prostate gland ovate, pallial portion short, ovate in section. Proximal pallial vas deferens having well-developed, reflexed loop. Penis (Figure 38G, H) large; base rectangular, slightly swollen along inner edge distally, smooth or weakly folded; filament short, broadly triangular, tapering to point, oblique; lobe slightly shorter than base, knoblike, distally narrowed, longitudinal. Terminal gland large, narrow, transverse, extending along much of outer edge of lobe, curving onto both surfaces. Penial gland filling proximal portion of filament and extending onto base, as wide as filament. Dg1 large, fairly broad, weakly raised, longitudinal, positioned near middle of base. Dorsal lobe bearing narrow gland basally. Ventral gland very small, circular-ovate, borne on raised swelling, sometimes longitudinal, positioned at base of lobe. Penial duct straight, near outer edge.

Type locality: Spring, Mud Meadow drainage, Humboldt County, Nevada, T. 40 N, R. 24 E, NW ¼ section 23. Holotype, USNM 873215 (Figure 21G), collected by J. Jerry Landye, 30 August 1979; paratypes, USNM 860707. The type locality area is the northernmost of a large series of thermal springs having broad outflows (e.g., Figure 3B). Water temperature at the sources of these springs was about 50°C. *Pyrgulopsis* ***notidicola*** was collected from moistened zones on emergent rocks (snails were much less abundant in the water). Downflow from source springs, where the water cooled to about 40°C, snails were still predominantly found out of the water. The madicolous habit of snails at the type locality was paralleled at the other two sites.

Remarks: This snail is distinguished from other species in the Soldier Meadows area by its more elongate shell with short spire, larger and more disjunct aperture, well-developed columellar shelf; smaller, globose bursa copulatrix; and penis with larger terminal gland, and very weak ventral gland.

Material examined: NEVADA. *Humboldt County:* Spring, Mud Meadow drainage, USNM 860707, USNM 873215, USNM 892048.—Spring (tub area), Mud Meadow drainage, T. 40 N, R. 24 E, NW ¼ section 23, USNM 874294.—Old gauge box, 0.8 km southwest of above, Mud Meadow drainage (Figure 3B), T. 40 N, R. 24 E, NW ¼ section 23, USNM 874286.

Pyrgulopsis ***vinyardi*** Hershler, sp. nov.

Vinyards pyrg

(Figures 8K, 21I, 39A–C)

Etymology: Named after Gary Vinyard (University of Nevada, Reno), in recognition of his assistance with field surveys in northwest Nevada.

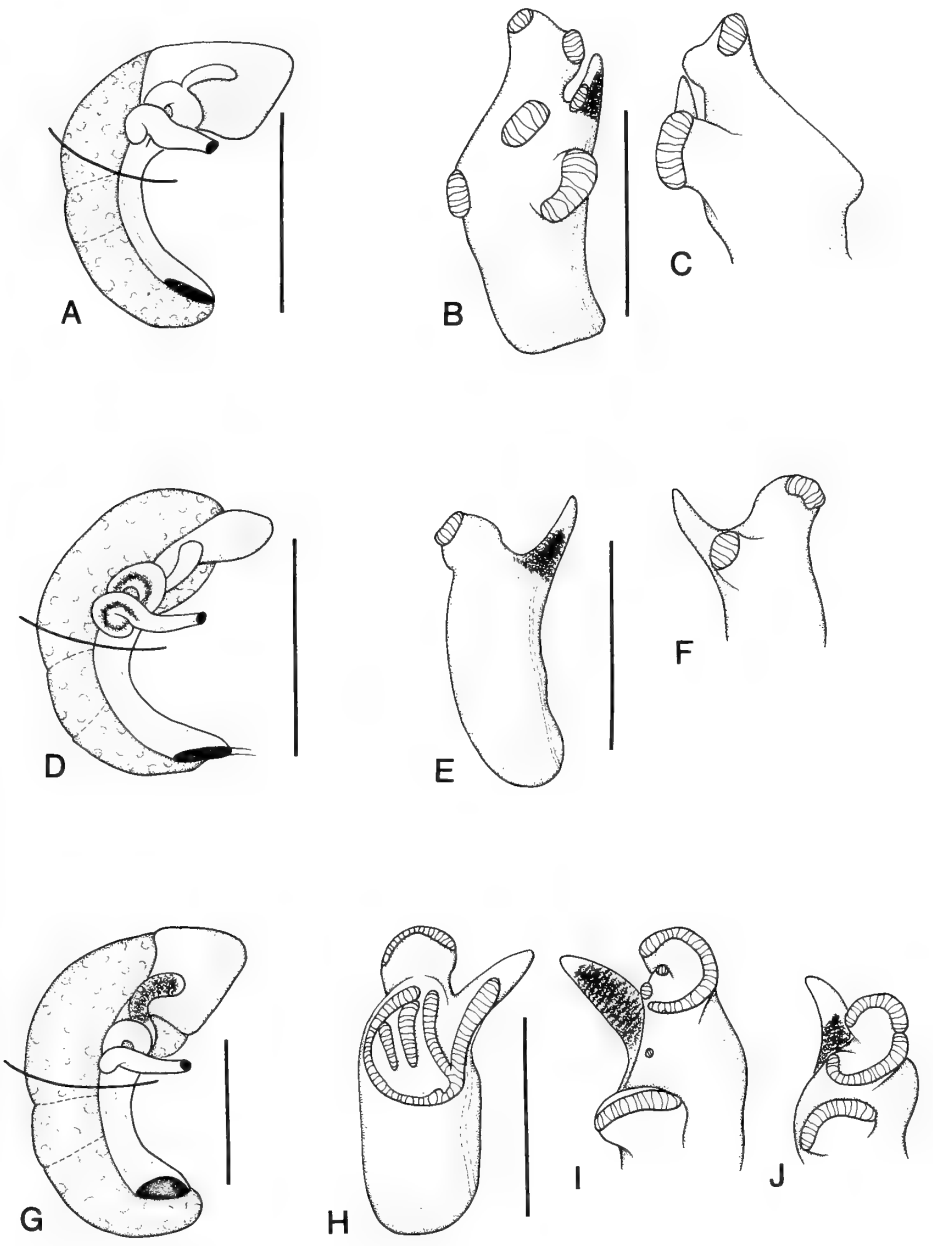


Figure 39

Genitalia of *Pyrgulopsis* species (A–C, *P. **vinyardi,*** USNM 874739; D–F, *P. **imperialis,*** USNM 874744; G–I, *P. **sadai,*** USNM 883857; J, *P. **sadai,*** USNM 883851). Bars = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis. Two examples of the ventral penis (I, J) are shown for *P. **sadai.***

Diagnosis: Small, with sub-globose to ovate-conic shell. Penis large, filament short, lobe medium length. Penial ornament a small terminal gland, small penial gland, large Dg1, small Dg2, small Dg3, additional dorsal gland on lobe, and large ventral gland.

Description: Shell (Figures 8K, 21I) sub-globose to ovate-conic, width/height, 75–92%; height, 1.6–2.0 mm; width, 1.3–1.6 mm; whorls, 3.5–4.0. Protoconch 1.2 whorls, diameter 0.21 mm, surface eroded. Teleoconch whorls medium to highly convex, shoulders well developed; body whorl often slightly disjunct behind the aperture. Aperture ovate, often expanded; broadly adnate or

slightly disjunct. Inner lip slightly thickened, sometimes having narrow columellar shelf. Outer lip thin, prosocline, weakly sinuate. Umbilicus narrowly rimate; umbilical region sometimes narrowly excavated. Periostracum yellow-tan.

Operculum ovate, dark amber; nucleus eccentric; dorsal surface weakly frilled. Attachment scar slightly thickened between nucleus and inner edge.

Radula 790 × 120 μm, with 63 rows of teeth. Central tooth 14 μm wide, with highly indented dorsal edge; lateral cusps, 6–7; central cusp long, narrow, daggerlike; basal cusps medium-sized. Basal process V-shaped, basal sockets medium depth. Lateral tooth formula 3-1-4(5); neck weakly flexed or absent; outer wing 210% of cutting edge length. Inner marginal teeth with 21–25 cusps (basal cusp enlarged); cutting edge occupying 35% of length of tooth. Outer marginal teeth with 25–30 cusps; cutting edge occupying 27% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles, snout, foot, neck light to medium grey-brown. Opercular lobe unpigmented or sometimes black along inner edge or all around. Pallial roof, visceral coil uniform black. Penial filament darkly pigmented along most of length.

Ctenidial filaments, 14, without pleats; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, centered slightly posterior to middle of ctenidium. Kidney opening white, thick. Rectum broadly overlapping genital ducts.

Ovary 0.75 whorl, filling less than 50% of digestive gland behind stomach, abutting or overlapping posterior stomach chamber. Distal female genitalia shown in Figure 39A. Albumen gland having short pallial component. Capsule gland longer than and as wide as albumen gland, ovate in section; rectal furrow well developed. Ventral channel slightly overlapping capsule gland; longitudinal fold weak. Genital aperture an elongate, terminal slit without anterior extension. Coiled oviduct a small posterior-oblique loop preceded by well-developed posterior twist. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix longer than and as wide as albumen gland, broadly ovate to pyriform, longitudinal, with almost entire length posterior to gland. Bursal duct originating from anterior edge at mid-line or slightly dorsal to mid-line, very short, medium width. Seminal receptacle small, narrow, overlapping middle of bursa copulatrix, entering dorsal portion of oviduct coil.

Testis 1.0–1.25 whorls, filling 50% of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland elongate bean-shaped, pallial portion medium, ovate in section. Proximal pallial vas deferens having well-developed, reflexed loop. Penis (Figure 39B, C) large; base rectangular, distally expanded along inner edge, smooth; filament short, narrow, tapering to point, slightly oblique; lobe as long or slightly longer than filament, knoblike, often distally bifurcate, longitudinal. Terminal gland small, sub-circular, transverse, curving, positioned along inner edge of distal lobe with most of length on ventral surface. Penial gland filling inner portion of proximal half of filament, 50% as wide as filament. Dg1 large, broad, rarely divided into two units, crescent-shaped, borne on prominent swelling, usually longitudinal, positioned a little behind base of filament. Dg2 dotlike or small (rarely absent), narrow, positioned medially along expanded inner edge. Dg3 small (rarely dotlike), circular, positioned along outer edge of lobe distally. Dorsal surface of lobe also bearing narrow, oblique-longitudinal gland medially. Ventral gland large, borne on very prominent swelling, longitudinal, positioned alongside base of filament. Penial duct straight, near outer edge.

Type locality: Spring, Willow Creek, 1.6 km southwest of Willow Creek Reservoir, Squaw Valley drainage, Elko County, Nevada, T. 39 N, R. 48 E, NE ¼ section 33. Holotype, USNM 874740 (Figure 211), collected by G. Vinyard, 5 June 1992; paratypes, USNM 860708. The type locality is a shallow, but broad rheocrene flowing out of a steep hillside.

Remarks: This snail closely resembles the group of locally endemic species in Soldier Meadows, especially *P. **militaris,*** which has a similar pattern of penial ornament and shape of oviduct coil. *Pyrgulopsis **vinyardi*** differs from this species in its larger shell aperture, frequent presence of a columellar shelf, and penis with smaller penial gland and prominent pedicel of the ventral gland. Animal from the type locality were highly parasitized, hence specimens from the second locality were used for anatomical study. The distribution of this species is shown in Figure 52.

Material examined: NEVADA. *Elko County:* Spring, source of Hot Creek, Squaw Valley drainage, T. 38 N, R. 48 E, SE ¼ section 11, USNM 874739.—Spring, Willow Creek, 1.6 km southwest of Willow Creek Reservoir, T. 39 N, R. 48 E, NE ¼ section 33, USNM 860708, USNM 874740.

*Pyrgulopsis **imperialis*** Hershler, sp. nov.

Kings River pyrg

(Figures 8L, 21J, K, 39D–F)

Etymology: From *imperialis* (Latin), of the empire or emperor; referring to the endemism of this species in Kings River Valley, Nevada.

Diagnosis: Small, with ovate- to narrow-conic shell. Penis large, filament and lobe medium length. Penial ornament a small length terminal gland and small ventral gland.

Description: Shell (Figures 8L, 21J, K) ovate- to narrow-

conic, near pupiform, width/height, 63–82%; height, 1.4–1.8 mm; width, 1.0–1.4 mm; whorls, 3.75–4.25. Protoconch 1.25 whorls, diameter 0.29 mm, initial 0.5–0.75 whorl finely wrinkled (mostly along inner edge), otherwise smooth. Teleoconch whorls slightly-moderately convex; body whorl often slightly disjunct behind the aperture. Aperture ovate, strongly angled above, disjunct. Inner lip thick, without columellar shelf. Outer lip slightly thickened, orthocline or weakly prosocline, slightly sinuate. Umbilicus narrowly rimate to perforate. Periostracum tan.

Operculum ovate, amber, nuclear region reddish; nucleus eccentric; dorsal surface smooth; outer margin having weak to well-developed rim. Attachment scar thick along inner edge, sometimes similarly so along a portion or remainder of perimeter.

Radula 760 × 125 μm, with 57 rows of teeth. Central tooth 14 μm wide, with highly indented dorsal edge; lateral cusps, 5–7 (sometimes fused dorsally); central cusp narrow, daggerlike; basal cusps small. Basal process V-shaped, basal sockets medium depth. Lateral tooth formula 3(4, 5)-1-5; neck weakly flexed; outer wing 275% of cutting edge length. Inner marginal teeth with 21–26 cusps; cutting edge occupying 36% of length of tooth. Outer marginal teeth with 28–31 cusps; cutting edge occupying 26% of length of tooth. Stomach longer than style sac; stomach chambers equal-sized; stomach caecum very small.

Cephalic tentacles, snout, foot, neck light to medium grey. Opercular lobe medium to dark grey-black all around, central area lighter. Pallial roof, visceral coil uniform black. Proximal half of penial filament darkly pigmented internally.

Ctenidial filaments, 12, without pleats; ctenidium overlapping pericardium posteriorly, osphradium small, narrow, centered slightly posterior to middle of ctenidium. Renal gland oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.5 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 39D. Albumen gland having short pallial component. Capsule gland as long and wide as albumen gland, ovate in section; rectal furrow moderately developed. Ventral channel moderately overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct of two overlapping, posterior-oblique or circular coils (anterior portion sometimes only twisted); oviduct walls invested with dark pigment. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copulatrix short, narrow, ovate or subglobular, longitudinal, with 50% of length posterior to gland. Bursal duct originating from anterior edge at midline, almost as long as bursa, medium width. Seminal receptacle small to medium-sized, narrow, overlapping anterior half of bursa.

Testis 1.25 whorls, filling more than 50% of digestive gland behind stomach, overlapping posterior and most of anterior stomach chambers. Prostate gland small, bean-shaped, pallial portion very short, narrowly ovate in section. Proximal pallial vas deferens straight or having weak bend. Penis (Figure 39E, F) large; base elongate-rectangular, smooth or weakly folded along inner edge; filament medium length and width, tapering to point, longitudinal or slightly oblique; lobe as long as filament, knoblike, longitudinal or slightly oblique. Terminal gland small, rectangular, sometimes divided into two units, sometimes weakly curved, tranverse, overlapping dorsal and ventral surfaces. Dotlike distal Dg3 seen in one specimen. Ventral gland small, sub-circular, borne on swelling alongside base of filament. Penial duct straight, near outer edge.

Type locality: Spring, south side of road, Thacker Pass, Kings River Valley, Humboldt County, Nevada, T. 44 N, R. 34 E, NE ¼ section 14 (Figure 53). Holotype, USNM 874207 (Figure 21J), collected by G. Vinyard, 24 June 1991; paratypes, USNM 860716. The type locality is a small, highly vegetated rheocrene arising from the side of a steep hill.

Remarks: This snail differs from other species in the genus in which the penis is solely ornamented with terminal and ventral glands by the combination of small size, fairly narrow shell, moderately elongate lateral wing on the lateral radular teeth, and pigmented coiled oviduct.

Material examined: NEVADA. *Humboldt County:* Spring, south side of road, Thacker Pass, USNM 860716, USNM 874207, USNM 874744.—Spring, north side of road, Thacker Pass, Kings River Valley, T. 44 N, R. 34 E, SE ¼ section 11, USNM 874211.

*Pyrgulopsis **sadai*** Hershler, sp. nov.

Sada's pyrg

(Figures 9A, 21L–N, 39G–J)

Etymology: Named after Don Sada, in recognition of his assistance with field surveys throughout the western portion of the Great Basin.

Diagnosis: Medium-sized, with sub-globose to ovate-conic shell. Penis large; filament and lobe medium length. Penial ornament a large terminal gland, large penial gland; large, fused Dg1–2, additional two to five dorsal glands, and two large ventral glands.

Description: Shell (Figures 9A, 21L–N) sub-globose to ovate-conic, width/height, 68–88%; height, 2.0–3.3 mm; width, 1.6–2.3 mm; whorls, 3.75–4.75. Protoconch 1.3 whorls, diameter 0.33 mm, surface near smooth. Teleoconch whorls medium convexity, shoulders well developed. Aperture ovate, usually broadly adnate. Inner lip thick in largest specimens, without columellar shelf. Out-

er lip thin, slightly prosocline, weakly sinuate. Umbilicus rimate to narrowly perforate. Periostracum tan-brown.

Operculum ovate, amber; nucleus eccentric; dorsal surface weakly frilled. Attachment scar broadly thickened along all or most of margin.

Radula 590 × 100 μm, with 60 rows of teeth. Central tooth 26 μm wide, with medium indented dorsal edge; lateral cusps, 5–7; central cusp medium width, daggerlike; basal cusps small, sometimes accompanied by minute cusps to outside. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 3-1-4(5); neck weakly flexed; outer wing 200% of cutting edge length. Inner marginal teeth with 25–29 cusps; cutting edge occupying 34% of length of tooth. Outer marginal teeth with 32–34 cusps; cutting edge occupying 25% of length of tooth. Stomach longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles light to medium grey-brown, sometimes almost black. Snout medium to dark grey-brown. Foot, neck light to medium grey-brown. Opercular lobe medium grey-black all around, central region lighter. Pallial roof, visceral coil medium grey to uniform black. Penial filament darkly pigmented.

Ctenidial filaments, 20, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, centered posterior to middle of ctenidial axis. Renal gland longitudinal or slightly oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.5–0.75 whorl, filling less than 50% of digestive gland behind stomach, slightly overlapping posterior stomach chamber. Distal female genitalia shown in Figure 39G. Albumen gland having short or no pallial component. Capsule gland slightly shorter to as long, as wide as albumen gland, sub-ovate in section; rectal furrow well developed. Ventral channel broadly overlapping capsule gland; longitudinal fold well developed. Genital aperture a sub-terminal pore without anterior extension. Coiled oviduct a posterior-oblique loop usually preceded by posterior-oblique twist or small loop. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length, slightly narrower than albumen gland, elongate-pyriform, longitudinal, with 50% of length posterior to gland. Bursal duct originating from anterior edge at mid-line, short, medium width to broad. Seminal receptacle small, narrow pouch, darkly pigmented internally, often folded, overlapping anterior half of bursa.

Testis 1.0–1.25 whorls, filling 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Prostate gland bean-shaped, pallial portion short, narrowly ovate in section. Proximal pallial vas deferens having well-developed, reflexed loop. Penis (Figure 39H-J) large; base rectangular, smooth; filament slightly shorter than base, medium width, tapering to point, longitudinal or slightly oblique; lobe shorter than filament, knoblike, longitudinal. Terminal gland large, narrow, crescentlike, sometimes comprising three abutting or closely adjacent units, transverse, curving onto ventral surface, abutting or fused with distal ventral gland. Penial gland filling most of length of filament, as wide as filament, extending onto base. Dg1 and Dg2 fused into large crescentlike unit crossing penis (proximal to filament) and extending distally where it may again cross the penis toward the filament (where it is borne on an obvious swelling); sometimes forming a completely closed circle, often also fused with penial gland. Dorsal penis having two to five additional elongate, longitudinal glands (sometimes fragmented and/or accompanied by one to two small, dotlike units) lying within circle formed by gland described above; glands may be variously fused with each other as well as with main crescentlike gland. (Dg3 was never seen as separate unit, but may be fused with Dg1-2, or possibly be represented by one of the longitudinal units enclosed by the above.) Proximal ventral gland large, narrow, borne on large swelling, transverse, positioned proximal to filament; distal gland slightly smaller, narrow, similarly borne on swelling, transverse. Space between ventral glands sometimes having dotlike gland. Penial duct straight, near outer edge.

Type locality: Spring, Moss Creek, Reese River Valley, Lander County, Nevada, T. 27 N, R. 44 E, SE ¼ section 16. Holotype, USNM 874397 (Figure 21L), collected by D. W. Sada, 10 September 1991; paratypes, USNM 860702. The type locality area is a complex of small, shallow (but having broad expanse) rheocrenes, all of which were seriously degraded by livestock (Figure 5A). Only a single spring in the complex contained this species, which was found in an area of less than 1 m^2.

Remarks: This snail resembles several other Great Basin species (*P. californiensis, P. longinqua, P. wongi*) in that the penis has a full complement of penial glands, with the main dorsal glands fused to form a U-shaped unit, within which are a series of additional longitudinal glands. *Pyrgulopsis* ***sadai*** further resembles *P. wongi* in having a distal, curved ventral gland which often is fused or abutting the terminal gland. *Pyrgulopsis* ***sadai*** differs from these species in having a moderately broad shell (that of *P. wongi* is broader while that of *P. californiensis* and *P. longinqua* is more attenuate) and strongly pigmented seminal receptacle. This species is found in the central part of the Lahontan Basin as well as in drainage of the Owyhee River (Figure 53).

Material examined: NEVADA. *Humboldt County:* Spring, Tony Creek, Silver State-Quinn River Valley, T. 40 N, R. 38 E, SW ¼ section 4, USNM 874754, USNM 874208, USNM 883995.—Maiden Springs, Little Owyhee River drainage, T. 45 N, R. 42 E, SE ¼ section 3, USNM 883900, USNM 883999. *Lander County:* Spring, Moss Creek (Figure 5A), USNM 860702, USNM 874397, USNM 883857.—Spring, Moss Creek, Reese River Valley, T. 27 N, R. 44 E, center section 13, USNM 883851.—Spring,

Willow Creek, Buffalo Valley, T. 32 N, R. 43 E, SE ¼ section 32, USNM 874408.—Spring, Daisy Creek, Buffalo Valley, T. 27 N, R. 41 E, SE ¼ section 9, USNM 874392. *Pershing County:* Buffalo Springs, Buffalo Valley, T. 30 N, R. 41 E, SW ¼ section 31, USNM 874388.

Pyrgulopsis ***augustae*** Hershler, sp. nov.

Elongate Cain Spring pyrg

(Figures 9B, 22A, 40A, B)

Etymology: Referring to local endemism of this snail in the foothills of the Augusta Mountains, Nevada.

Diagnosis: Medium-sized, with narrow-conic shell. Penis medium-sized, bladelike; filament short, lobe absent. Penial ornament absent.

Description: Shell (Figures 9B, 22A) narrow-conic, width/height, 60–66%; height, 2.1–2.6 mm; width, 1.3–1.6 mm; whorls, 4.25–5.25. Protoconch 1.25 whorls, diameter 0.29 mm, early portion finely wrinkled, later surface near smooth, entire surface often eroded. Teleoconch whorls slightly convex, sometimes almost flat, narrowly shouldered; body whorl often slightly disjunct behind the aperture. Aperture ovate, strongly angled above; broadly adnate or slightly disjunct. Inner lip slightly thickened in largest specimens, without columellar shelf. Outer lip thin, orthocline or slightly prosocline, without sinuation. Umbilicus rimate, shell rarely anomphalous. Periostracum light tan.

Operculum ovate, light amber; nucleus eccentric; dorsal surface frilled; outer margin sometimes having weak rim. Attachment scar thickened between nucleus and inner edge.

Radula 840 × 135 μm, with 53 rows of teeth. Central tooth 21 μm wide, with medium indented dorsal edge; lateral cusps, 4–5; central cusp medium width, dagger-like; basal cusps medium-sized. Basal tongue broad V-shaped, sometimes terminating with distinct, small, U-shaped component; basal sockets medium depth. Lateral tooth formula 2(3)-1-3(4); neck weakly flexed; outer wing 160% of cutting edge length. Inner marginal teeth with 19–22 cusps; cutting edge occupying 34% of length of tooth. Outer marginal teeth with 22–28 cusps; cutting edge occupying 27% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented, but usually having light to medium grey-brown stripe proximally. Snout nearly unpigmented to medium brown. Foot unpigmented or very light brown. Opercular lobe usually having medium grey streak along inner edge, sometimes similarly pigmented along sides. Neck unpigmented except for scattered grey-brown granules to medium grey. Pallial roof, visceral coil medium to dark grey-brown, pigment lighter on ventral surface. Distal base of penis and proximal filament having medium (internal) brown pigment.

Ctenidial filaments, 17, weakly pleated; ctenidium connected to pericardium by short efferent vessel. Osphradium small, narrowly ovate, centered slightly posterior to middle of ctenidium. Renal gland longitudinal; kidney opening grey-white. Rectum broadly overlapping pallial oviduct, slightly overlapping prostate gland.

Ovary 0.75 whorl, filling less than 50% of digestive gland behind stomach, slightly overlapping posterior stomach chamber. Distal female genitalia shown in Figure 40A. Albumen gland having short pallial component. Capsule gland shorter and narrower than albumen gland, ovate in section; rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct of two small, overlapping posterior-oblique loops. Oviduct and bursal duct joining just behind pallial wall. Bursa copulatrix short, medium width, ovate-pyriform, longitudinal or oblique, 50% of length posterior to gland; dorsal edge sometimes slightly overlapped by gland. Bursal duct originating from anterior edge at or lateral to mid-line, as long as bursa, medium width. Seminal receptacle small, narrow, sometimes folded, overlapping anterior bursa or proximal portion of bursal duct.

Testis 1.5 whorls, filling 50% of digestive gland behind stomach, overlapping posterior and part of anterior stomach chambers. Prostate gland very small, bean-shaped, pallial portion short, narrowly ovate in section. Proximal pallial vas deferens straight or having small, weak bend. Penis (Figure 40B) medium-sized; base elongate-rectangular, smooth; filament short, tapering to point, medium width, longitudinal, weakly distinguished from base by slight constriction; lobe absent, distal edge of penis gently tapering; glands absent. Penial duct straight, near outer edge.

Type locality: Cain Spring, Antelope Valley, Lander County, Nevada, T. 25 N, R. 40 E, SW ¼ section 5 (Figure 53). Holotype, USNM 874402 (Figure 22A), collected by D. W. Sada, 10 September 1991; paratypes, USNM 860687. The type locality is a small rheocrene in which *Pyrgulopsis* ***augustae*** co-occurs with *P.* ***pictilis*** (described below).

Remarks: This species is contrasted with *P.* ***dixensis*** above.

Material examined: NEVADA. *Lander County:* Cain Spring, USNM 860687, USNM 874402.

Pyrgulopsis ***pictilis*** Hershler, sp. nov.

Ovate Cain Spring pyrg

(Figures 9C, 22B, C, 40C–E)

Etymology: From *pictilis* (Latin), colored; referred to the strong pigmentation of the female seminal receptacle in this species.

Diagnosis: Medium-sized, with broadly to ovate-conic

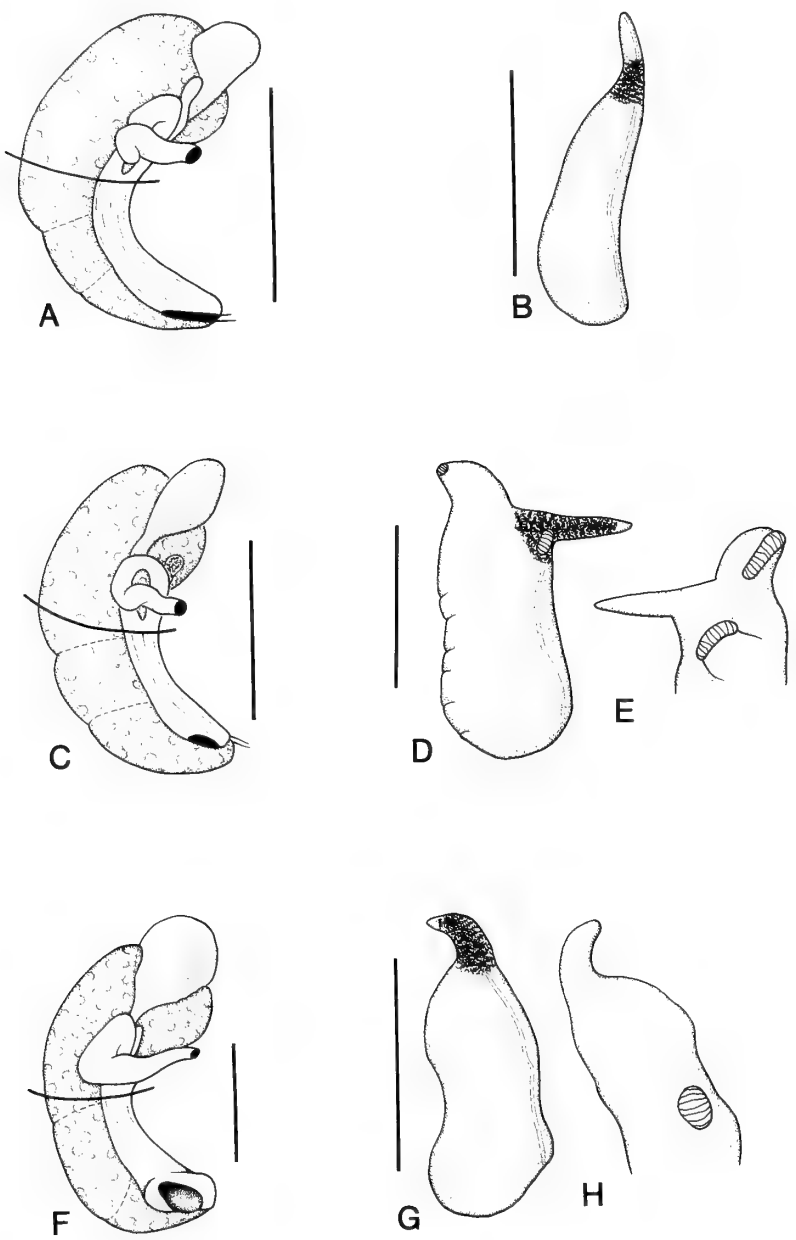


Figure 40

Genitalia of *Pyrgulopsis* species (A, B, ***P. augustae,*** USNM 860687; C–E, ***P. pictilis,*** USNM 860713; F–H, ***P. basiglans,*** USNM 860692). A–E. Bars = 0.5 mm. F. Bar = 0.25 mm. G, H. Bar = 0.25 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis (not shown for ***P. augustae*** as this species lacks ornament).

shell. Penis large; filament and lobe medium length. Penial ornament a medium-sized terminal gland, very small penial gland, and small ventral gland.

Description: Shell (Figures 9C, 22B, C) broadly to ovate-conic, width/height, 77–86%; height, 2.0–2.7 mm; width, 1.7–2.2 mm; whorls, 4.0–4.75. Protoconch 1.25 whorls, diameter 0.33 mm; surface smooth except for occasional very weak wrinkling at apex. Teleoconch whorls highly convex, often broadly shouldered. Aperture ovate, broadly adnate or narrowly disjunct. Inner lip slightly thick, sometimes having narrow columellar shelf. Outer lip thin, prosocline, without sinuation. Umbilicus rimate or narrowly perforate. Periostracum tan.

Operculum ovate, amber, nuclear region darker; nucle-

us eccentric; dorsal surface smooth; outer margin having weak rim. Attachment scar slightly thickened between nucleus and inner edge.

Radula 640 × 110 μm, with 54 rows of teeth. Central tooth 28 μm wide, with highly indented dorsal edge; lateral cusps, 6–7; central cusp medium width, daggerlike, basal cusps medium-sized. Basal tongue broad V-shaped, basal sockets medium depth. Lateral tooth formula 3(4)-1-4(5); neck weakly flexed, outer wing 167% of cutting edge length. Inner marginal teeth with 26–29 cusps; cutting edge occupying 35% of length of tooth. Outer marginal teeth with 33–39 cusps; cutting edge occupying 25% of length of tooth. Stomach as long as style sac; anterior chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles nearly unpigmented to light brown. Snout light grey-brown. Foot light to medium grey-brown. Opercular lobe dark along inner edge, sometimes all around. Neck light to medium grey. Pallial roof, visceral coil dark brown-black, pigment lighter on genital ducts. Penial filament darkly pigmented along most of length; distal penis adjacent to filament similarly pigmented. Penial lobe sometimes having scattered black granules.

Ctenidial filaments, 17, pleated, ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, centered posterior to middle of ctenidium. Renal gland oblique; kidney opening slightly thickened. Rectum broadly overlapping pallial oviduct, slightly overlapping prostate gland.

Ovary 0.75–1.25 whorl, filling 50% or slightly less of digestive gland behind stomach, abutting posterior edge of stomach anteriorly. Distal female genitalia shown in Figure 40C. Albumen gland having very short pallial component. Capsule gland slightly shorter, narrower than albumen gland, ovate in section; rectal furrow medium depth. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a posterior-oblique loop preceded by weak twist or small posterior-oblique coil. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copulatrix short, medium width, narrowly ovate, longitudinal, 33–50% of length posterior to gland. Bursal duct originating from anterior edge at or near mid-line, 50–67% length of bursa, medium width. Seminal receptacle small, pouchlike, darkly pigmented, overlapping or ventral to proximal bursal duct and (sometimes) anteriormost bursa.

Testis 1.5 whorls, filling more than 50% of digestive gland behind stomach, overlapping posterior and part of anterior stomach chamber. Prostate gland very small, ovate or weakly bean-shaped, entirely visceral or with very short pallial portion, narrowly ovate in section. Proximal pallial vas deferens having well-developed loop. Penis (Figure 40D, E) large; base elongate-rectangular, weakly folded; filament medium length, narrow, tapering to point, slightly oblique; lobe medium length, clublike, longitudinal. Terminal gland medium-sized, narrow, slightly curved, transverse, largely on ventral surface. Penial gland small, 50% as wide as filament, positioned along outer edge of proximal filament, sometimes slightly overlapping base distally. Single specimen having dotlike gland along outer edge of penis distally (corresponding to Dg2). Ventral gland small (absent in one specimen), transverse or oblique, borne on swelling, positioned alongside base of filament. Penial duct straight, near outer edge.

Type locality: Cain Spring, Antelope Valley, Lander County, Nevada, T. 25 N, R. 40 E, SW ¼ section 5 (Figure 53). Holotype, USNM 874401 (Figure 22B), collected by D. Sada, 10 September 1991; paratypes, USNM 860713.

Remarks: This species closely resembles *P.* ***humboldtensis*** (described below) in penial form and pattern of ornament, but is distinguished by its weaker operculum attachment scar, more numerous cusps on the marginal radular teeth, broader penial filament, longer bursal duct, and pigmented seminal receptacle. The single sample of this species contained only three males.

Material examined: NEVADA. *Lander County:* Cain Spring, USNM 860713, USNM 874401.

Pyrgulopsis ***basiglans*** Hershler sp. nov.

Large gland Carico pyrg

(Figures 9D, 13D, 22D, 40F–H)

Etymology: From *basis* (Latin), bottom; *glans,* gland; referring to the unusual basal position of the ventral gland of the penis of this species.

Diagnosis: Small, with sub-globose to ovate-conic shell. Penis large, filament short, lobe absent. Penial ornament a medium-sized ventral gland.

Description: Shell (Figures 9D, 22D) sub-globose to ovate-conic, width/height, 73–87%; height, 1.3–1.8 mm; width, 1.1–1.3 mm; whorls, 3.5–4.5. Protoconch 1.2–1.25 whorls, diameter 0.28 mm, surface smooth except for fine wrinkling near apex and widely spaced, weak spiral striae on final 0.5 whorl. Teleoconch whorls highly convex, shoulders well developed, often broad; body whorl often slightly disjunct behind the aperture. Aperture ovate; narrowly adnate or disjunct. Inner lip thin, without columellar shelf. Outer lip thin, prosocline, without sinuation. Umbilicus perforate. Periostracum tan.

Operculum (Figure 13D) ovate, amber, nuclear region reddish; nucleus eccentric; dorsal surface frilled; outer margin having weak rim. Attachment scar broadly thickened all around.

Radula 760 × 120 μm, with 67 rows of teeth. Central tooth 17 μm wide, with highly indented dorsal edge; lateral cusps, 5–7; central cusp narrow, daggerlike; basal

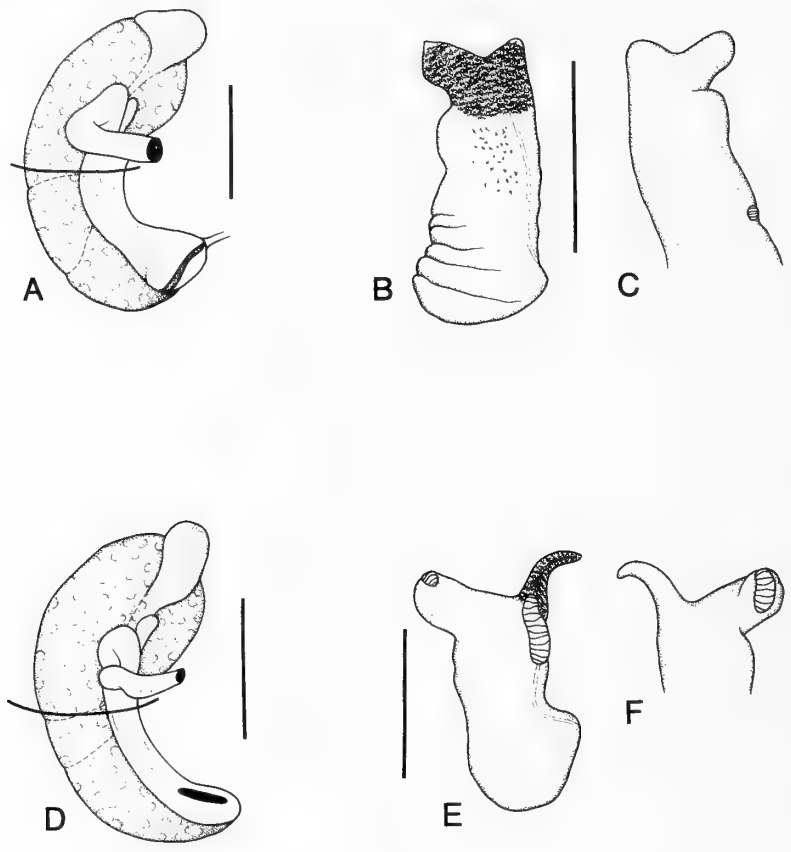


Figure 41

Genitalia of *Pyrgulopsis* species (A–C, *P.* ***bifurcata,*** USNM 860693; D–F, *P.* ***pellita,*** USNM 860715). A. Bar = 0.25 mm. B–F. Bars = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis. Note the bifurcate penial filament of *P.* ***bifurcata.***

cusps medium-sized. Basal tongue broad V-shaped, basal sockets deep. Lateral tooth formula 4(5)-1-4(5); neck weakly flexed or absent; outer wing 230% of cutting edge length. Inner marginal teeth with 24–30 cusps; cutting edge occupying 33% of length of tooth. Outer marginal teeth with 29–34 cusps; cutting edge occupying 25% of length of tooth. Stomach longer than style sac; anterior stomach chamber larger than posterior chamber; stomch chamber very small.

Cephalic tentacles, snout light to medium grey-brown. Foot, neck light grey. Opercular lobe light to medium grey-brown, pigment diffuse. Pallial roof, visceral coil uniform black. Penial filament darkly pigmented internally.

Ctenidial filaments, 12, weakly pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, centered well posterior to middle of ctenidium. Renal gland slightly oblique; kidney opening grey. Rectum broadly overlapping genital ducts.

Ovary 0.5 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 40F. Albumen gland having short or no pallial component. Capsule gland as long, but narrower than albumen gland, subcircular in section, rectal furrow absent. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a large terminal pore mounted on a swollen and slightly raised papilla; anterior extension absent. Coiled oviduct a posterior-oblique loop sometimes kinked at mid-length. Oviduct and bursal duct joining just behind pallial wall. Bursa copulatrix medium length and width, ovate, longitudinal, sometimes overlapped by gland anteriorly, 50% of length posterior to gland. Bursal duct originating from anterior edge at midline, 50–75% length of bursa, medium width (often expanded distally), sometimes overlapped by albumen gland proximally. Seminal receptacle minute, narrow, overlapping proximal bursal duct.

Testis 1.0 whorl, filling more than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Prostate gland elongate bean-shaped, pallial portion short, ovate in section. Proximal pallial vas deferens having well-developed, weakly reflexed loop. Pe-

nis (Figure 40G, H) large; base rectangular, inner edge usually expanded distally, smooth; filament short, curved, medium width, tapering to point, longitudinal; lobe absent. Distal edge of penis tapering toward base of filament. Ventral gland medium-sized, ovate, longitudinal, positioned near inner edge proximally. Penial duct straight, near outer edge.

Type locality: Spring, Cooks Creek, Carico Lake Basin, Lander County, Nevada, T. 27 N, R. 45 E, NE¼ section 27. Holotype, USNM 874280 (Figure 22D), collected by R. Hershler, 26 July 1991; paratypes, USNM 860692. The type locality is a broad rheocrene heavily impacted by livestock grazing.

Remarks: Among species having penial ornament solely consisting of a superficial ventral gland, this species and *Pyrgulopsis* ***bifurcata*** (described next), also locally endemic in Carico Lake Basin, compose a distinct group in which the ventral gland is small and positioned near the inner edge proximally. These species are further united by small, broad to ovate-conic shell, moderately sculptured protoconch having spiral striae on later portion, thick operculum attachment scar; deeply indented central radular teeth with slender, elongate central cusps and deep basal sockets; and distal female genitalia having a simple oviduct coil; very small, narrow, seminal receptacle; and raised and expanded distal end of ventral channel. *Pyrgulopsis* ***basiglans*** differs from *P.* ***bifurcata*** in the larger ventral gland on the penis, absence of a penial lobe, and ovate (not pyriform) bursa copulatrix. The distribution of this species is shown in Figure 53.

Material examined: NEVADA. *Lander County:* Spring, Cooks Creek, USNM 860692, USNM 874280.—Springs, southeast side of Carico Lake, Carico Lake Basin, T. 26 N, R. 45 E, NE¼ section 15, USNM 874304.

Pyrgulopsis ***bifurcata*** Hershler, sp. nov.

Small gland Carico pyrg

(Figures 9E, 22E, 41A–C)

Etymology: From *furcatus* (Latin), forked; referring to the unusual, bifurcate aspect of the distal end of the penis in this species.

Diagnosis: Small, with broadly- to ovate-conic shell. Penis large, filament and lobe short. Penial ornament a very small ventral gland.

Description: Shell (Figures 9E, 22E) broadly to ovate-conic, width/height, 70–83%; height, 1.3–1.8 mm; width, 1.0–1.3 mm; whorls, 4.0–4.5. Protoconch 1.3 whorls, diameter 0.25 mm, initial 0.75 whorl finely wrinkled, later portion smooth except for weak spiral striae. Teleoconch whorls highly convex, shoulders well developed; body whorl often slightly disjunct behind the aperture. Aperture sub-circular, narrowly adnate or, more commonly, disjunct. Inner lip thin, without columellar shelf. Outer lip thin, prosocline, without sinuation. Umbilicus perforate. Periostracum tan.

Operculum ovate, light amber, nuclear region dark amber; nucleus eccentric; dorsal surface nearly smooth. Attachment scar thick all around.

Radula 790 × 130 μm, with 63 rows of teeth. Central tooth 19 μm wide, with highly indented dorsal edge; lateral cusps, 4–7; central cusp long, narrow, daggerlike; basal cusps small. Basal tongue V-shaped, basal sockets deep. Lateral tooth formula 3(4)-1-4(5); neck straight; outer wing 230% of cutting edge length. Inner marginal teeth with 20–29 cusps; cutting edge occupying 33% of length of tooth. Outer marginal teeth with 26–32 cusps; cutting edge occupying 22% of length of tooth. Stomach longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum very small.

Cephalic tentacles unpigmented, except for light grey patch proximally, to medium grey-brown. Snout, foot, light to medium grey-brown. Opercular lobe pigment diffuse, light to medium grey, or dark all around. Neck unpigmented, except for scattered granules, to medium grey-brown. Pallial roof, visceral coil dark brown, pigment sometimes uniform. Penial filament and lobe (and small portion of distal penis) darkly pigmented internally; base pigmented with scattered dark granules.

Ctenidial filaments, 11, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, centered well posterior to middle of ctenidium. Renal gland slightly oblique; renal opening grey. Rectum broadly overlapping pallial oviduct, slightly overlapping prostate gland.

Ovary 0.5 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 41A. Albumen gland having very short or no pallial component. Capsule gland as long or longer, but slightly narrower than albumen gland, sub-circular in section; rectal furrow weak. Ventral channel broadly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit mounted on a swollen and weakly raised papilla; anterior extension short. Coiled oviduct a posterior-oblique loop, often kinked at mid-length. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix short, slightly narrower than albumen gland, ovate-pyriform, longitudinal, with 66% of length posterior to gland. Bursal duct originating from anterior edge at mid-line, proximal portion overlapped by albumen gland, slightly shorter or as long as bursa, narrow to medium width. Seminal receptacle very small, narrow.

Testis 1.25 whorls, filling more than 50% of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland elongate bean-shaped, pallial portion short, ovate in section. Proximal pallial vas deferens having gentle bend. Penis (Figure 41B, C) large; base elongate-rectangular, strongly folded proximally; filament

short, broadly triangular, tapering to point, oblique (angling toward inner edge); lobe slightly shorter than filament, triangular, arising from outer edge of penis, oblique. Ventral gland very small (rarely absent), circular, positioned along inner edge near base. Penial duct straight and near outer edge proximally, bending toward outer edge of filament distally, coursing along edge and terminating at tip of filament.

Type locality: Springs, west of Carico Lake, Carico Lake Basin, Lander County, Nevada, T. 26 N, R. 45 E, NW¼ section 16 (Figure 53). Holotype, USNM 874306 (Figure 22E), collected by R. Hershler, 24 July 1991; paratypes, USNM 860693. The type locality consists of two adjacent, thermal (23.5°C.) rheocrenes that feed a small stream. The area is highly impacted by cattle. Snails were collected about 7 m downflow from the spring sources.

Remarks: This species is contrasted with *P.* ***basiglans*** above.

Material examined: NEVADA. *Lander County:* Springs, west of Carico Lake, USNM 860693, USNM 874306.

Pyrgulopsis ***pellita*** Hershler, sp. nov.

Antelope Valley pyrg

(Figures 9F, 22F, 41D–F)

Etymology: From *pellitus* (Latin), covered with skin; referring to the thick periostracum covering the shell of this species.

Diagnosis: Medium-sized, with ovate- to narrow-conic shell. Penis large; filament and lobe medium length. Penial ornament a medium-sized terminal gland and large Dg1.

Description: Shell (Figures 9F, 22F) ovate- to narrow-conic, apex often eroded, width/height, 70–84%; height, 2.2–3.0 mm; width, 1.7–2.1 mm; whorls, 3.75–4.5. Protoconch 1.4 whorls, diameter 0.38 mm, weakly wrinkled at apex, otherwise smooth. Teleoconch whorls medium to high convexity, shoulders weakly developed or absent; sculpture including numerous faint spiral lirae; body whorl often slightly disjunct behind the aperture in largest specimens. Aperture ovate, angled above; adnate or slightly disjunct. Inner lip slightly thickened, without columellar shelf. Outer lip thin, slightly prosocline, without sinuation. Umbilicus rimate. Periostracum dark red-brown.

Operculum ovate, dark amber; nucleus eccentric; dorsal surface weakly frilled. Attachment scar thick all around.

Radula 570 × 95 μm, with 62 rows of teeth. Central tooth 29 μm wide, with highly indented dorsal edge; lateral cusps, 6–9; central cusp medium width, daggerlike; basal cusps small. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 4(5)-1-5(6); neck weakly flexed; outer wing 175% of cutting edge length. Inner marginal teeth with 26–32 cusps; cutting edge occupying 35% of length of tooth. Outer marginal teeth with 37–42 cusps; cutting edge occupying 26% of length of tooth. Stomach slightly longer than style sac; stomach chambers equal-sized; stomach caecum small.

Cephalic tentacles light to medium grey-brown; pigment concentrated proximally. Snout light to medium grey-brown. Foot light grey-brown. Opercular lobe usually dark along inner edge, unpigmented or diffusely pigmented elsewhere. Neck unpigmented, except for scattered grey granules, to medium grey-brown. Pallial roof, visceral coil uniform dark brown-black. Penial filament darkly pigmented internally, lobe and distal penis sometimes pigmented with scattered black granules.

Ctenidial filaments, 16, without pleats; ctenidium overlapping pericardium posteriorly. Osphradium small, narrowly ovate, positioned centrally or slightly posterior to middle of ctenidium. Renal gland slightly oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.75–1.0 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 41D. Albumen gland having very short or no pallial component. Capsule gland as long or slightly longer, but narrower than albumen gland, ovate in section; rectal furrow well developed. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit without anterior extension. Coiled oviduct a tight, posterior-oblique loop preceded by proximal twist or small anterior-oblique bend. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix short, narrow, narrowly ovate, anterior end weakly distinguished from duct, longitudinal, with 25–50% of length posterior to gland, sometimes slightly overlapped on sides by gland. Bursal duct originating from anterior edge at mid-line and close to oviduct, 50–100% length of bursa, sometimes almost as wide as bursa, usually overlapped proximally (completely or along sides) by albumen gland. Seminal receptacle small, pouchlike, overlapping proximal bursal duct or anteriormost portion of bursa.

Testis 1.25 whorls, filling more than 50% of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland small, bean-shaped, pallial portion short, ovate in section. Proximal pallial vas deferens having broad bend. Penis (Figure 41E, F) large; base rectangular, smooth; filament medium length and width, tapering to point, slightly oblique; lobe slightly shorter to slightly longer than filament, cylindrical, longitudinal or slightly oblique. Terminal gland medium-sized, narrow, slightly curved, largely on ventral surface. Dg1 large, rarely greatly reduced, slightly raised, positioned just behind or slightly overlapping base of filament. Ventral penis sometimes bearing raised, glandular dot

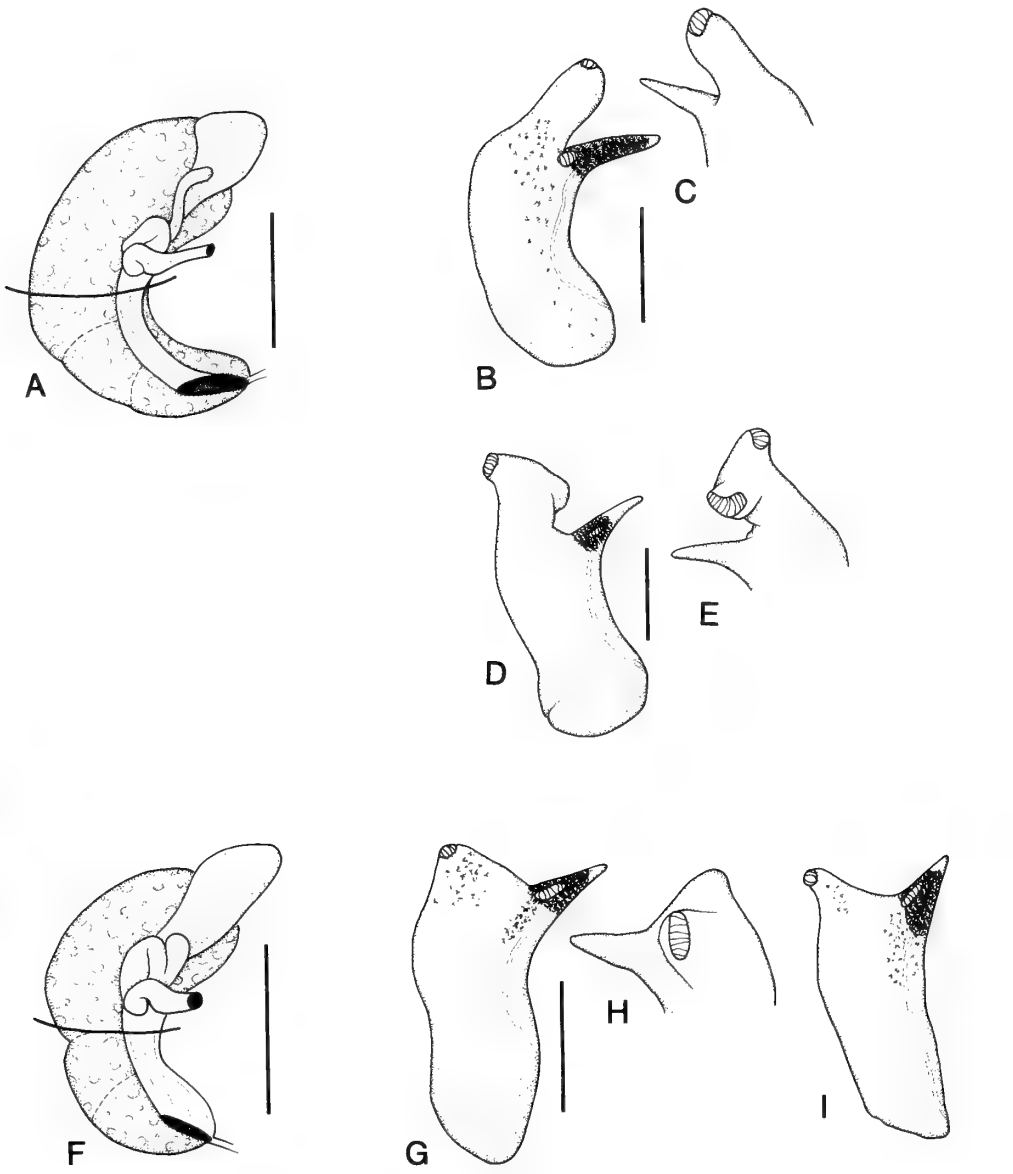


Figure 42

Genitalia of *Pyrgulopsis* species (A–C, *P.* ***leporina,*** USNM 860717; D, E, *P.* ***leporina,*** USNM 874315; F–I, *P.* ***humboldtensis,*** USNM 860718). Bars = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis. Two sets of penes (B, C; D, E) are shown for *P.* ***leporina,*** and two examples of the dorsal penis (G, I) are shown for *P.* ***humboldtensis.***

alongside base of filament. Penial duct straight, near outer edge.

Type locality: Sullivan Spring, Antelope Valley, Eureka County, Nevada, T. 17 N, R. 50 E, NE ¼ section 31 (Figure 53). Holotype, USNM 883850 (Figure 22F), collected by R. Hershler and P. Hovingh, 7 July 1994; paratypes, USNM 860715. The type locality is a small limnocrene (ca. 2 m wide) surrounded by an old fence. Snails were collected from the pool outflow.

Remarks: Among the group of species having penial ornament that includes an elongate Dg1 positioned just behind the penial filament, this species is unique in also having a terminal gland, but no other ornament.

Material examined: NEVADA. *Eureka County:* Sullivan Spring, USNM 860715, USNM 874383, USNM 883850.

Pyrgulopsis ***leporina*** Hershler, sp. nov.

Elko pyrg

(Figures 9G, 22G, 42A–E)

Etymology: From *leporinus* (Latin), of hares; referring to location of the type locality in Rabbit Creek drainage, Nevada.

Diagnosis: Medium-sized to large, with ovate- to narrow-conic shell. Penis large; filament medium length, lobe short-medium length. Penial ornament a small terminal gland, and very small penial gland.

Description: Shell (Figures 9G, 22G) ovate- to narrow-conic, apex often eroded, width/height, 64–78%; height, 3.2–4.8 mm; width, 2.3–3.0 mm; whorls, 3.5–5.25. Protoconch 1.2–1.25 whorls, diameter 0.46 mm, weakly wrinkled at apex and sculptured with faint spiral striae on later portion, otherwise smooth. Teleoconch whorls medium convexity, weakly shouldered; body whorl often slightly disjunct behind the aperture. Aperture ovate, usually slightly disjunct. Inner lip thin, without columellar shelf. Outer lip thin, orthocline or slightly prosocline, without sinuation. Umbilicus narrowly rimate to perforate. Periostracum tan, covered with thick brown deposit.

Operculum ovate, dark amber-red; nucleus eccentric; dorsal surface weakly frilled; outer margin sometimes having weak rim. Attachment scar thick all around.

Radula 970 × 130 μm, with 62 rows of teeth. Central tooth 42 μm wide, with medium indented dorsal edge; lateral cusps, 4–7; central cusp broad, spoonlike, considerably longer than laterals; basal cusps medium-sized. Basal process broad V-shaped, shorter than lateral margins, basal sockets medium depth. Lateral tooth formula 2(3)-1-3(4); neck medium flexed; outer wing 170% of cutting edge length. Inner marginal teeth with 24–27 cusps; cutting edge occupying 31% of length of tooth. Outer marginal teeth with 33–38 cusps; cutting edge occupying 25% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented to medium grey-brown, pigmented concentrated proximally. Snout light to medium grey-brown. Foot unpigmented (except for scattered grey granules) to medium grey-brown. Opercular lobe usually dark along inner edge. Neck unpigmented (except for scattered grey granules) to medium grey-brown. Pallial roof, visceral coil dark grey-brown or black, almost uniformly so. Penial filament darkly pigmented internally; dorsal penis otherwise lightly pigmented with scattered grey granules.

Ctenidial filaments, 19, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrowly ovate, centered slightly posterior to middle of ctenidium. Renal gland longitudinal or slightly oblique; kidney opening grey-white. Rectum broadly overlapping pallial oviduct, slightly or not overlapping prostate gland.

Ovary 0.75 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 42A. Albumen gland having short pallial component. Capsule gland shorter, narrower than albumen gland, ovate in section; rectal furrow absent. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct of two overlapping, posterior-oblique loops. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, ovate-pyriform, anterior portion often poorly distinguished from duct, longitudinal, with 50% of length posterior to gland, sometimes partly overlapped by gland. Bursal duct originating from anterior edge at mid-line, usually at least as long as bursa, medium width, usually lying in depression within albumen gland. Seminal receptacle small, elongate pouch, folded, overlapping anterior portion of bursa or proximal portion of bursal duct.

Testis 2.0 whorls, filling almost all of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland small, ovate or bean-shaped, pallial portion very short, narrowly ovate in section. Proximal pallial vas deferens having weak bend or well-developed, reflexed loop. Penis (Figure 42B-E) large; base rectangular, smooth; filament shorter than base, medium width, tapering to point, slightly oblique; lobe slightly longer to slightly shorter than filament, rectangular, often bifurcate distally, longitudinal. Terminal gland small, narrow, often divided into two widely spaced units (with associated bifurcation of distal lobe), rarely trifurcate, transverse, largely on ventral surface. Penial gland very small, restricted to proximal portion of filament, narrower than filament. Dorsal penis sometimes having one to two dotlike units near base of lobe. Small, raised ventral gland seen in one specimen. Penial duct straight, near outer edge.

Type locality: Springs, Rabbit Creek, Humboldt River drainage, Elko County, Nevada, T. 33 N, R. 57 E, SE ¼ section 2. Holotype, USNM 874336 (Figure 22G), collected by R. Hershler, 30 July 1991; paratypes, USNM 860717. The type locality is a shallow, moderately broad (7 m) helocrene slightly impacted by cattle.

Remarks: This species most closely resembles *P.* ***serrata,*** from Steptoe Valley, with which it shares penial ornament of small penial and terminal glands. *Pyrgulopsis* ***leporina*** differs from the above in its much larger central radular teeth, spoon-shaped central cusps on these teeth, larger penial lobe, and larger bursa copulatrix. The distribution of this snail is shown in Figure 53.

Material examined: NEVADA. *Elko County:* Springs,

Rabbitt Creek, USNM 860717, USNM 874336.—Persons Spring, Ruby Valley, T. 34 N, R. 60 E, NW ¼ section 26, USNM 874315.

Pyrgulopsis ***humboldtensis*** Hershler, sp. nov.

Humboldt pyrg

(Figures 9H, 13E, 22H–J, 42F–I)

Etymology: Referring to distribution of this species in Humboldt River drainage, Nevada.

Diagnosis: Medium-sized, with sub-globose to ovate-conic shell. Penis large; filament and lobe short. Penial ornament a small terminal gland, very small penial gland, and medium-sized ventral gland.

Description: Shell (Figures 9H, 22H–J) sub-globose to ovate-conic, width/height, 70–91%; height, 2.0–3.1 mm; width, 1.7–2.3 mm; whorls, 3.75–4.5. Protoconch 1.3–1.4 whorls, diameter 0.40 mm, initial 0.5–0.75 whorl weakly wrinkled (mostly along inner edge), otherwise smooth. Teleoconch whorls highly convex, broadly shouldered; body whorl often slightly disjunct behind the aperture. Aperture ovate, usually disjunct. Inner lip complete, thin, without columellar shelf. Outer lip thin, weakly prosocline, without sinuation. Umbilicus perforate. Periostracum brown.

Operculum (Figure 13E) ovate, dark amber; nucleus eccentric; dorsal surface weakly frilled. Attachment scar thick all around.

Radula 760 × 125 μm, with 54 rows of teeth. Central tooth 31 μm wide, with highly indented dorsal edge; lateral cusps, 5–6; central cusp narrow to medium width, daggerlike, basal cusps small, sometimes accompanied by thickening to outside. Basal process V-shaped, basal sockets medium depth. Lateral tooth formula 3-1-4(5); neck straight or weakly flexed; outer wing 200% of cutting edge length. Inner marginal teeth with 19–21 cusps; cutting edge occupying 32% of length of tooth. Outer marginal teeth with 28–32 cusps; cutting edge occupying 25% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles, snout light to medium grey-brown. Foot medium to dark grey-brown. Opercular lobe dark along inner edge, sometimes all around. Neck light to medium grey. Pallial roof, visceral coil dark brown-black, pigment sometimes uniformly dark. Proximal 67% of penial filament darkly pigmented; distal penis and lobe often medium-darkly pigmented.

Ctenidial filaments, 19, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrowly ovate, centered slightly posterior to middle of ctenidium. Renal gland strongly oblique; kidney opening slightly thickened. Rectum broadly overlapping genital ducts.

Ovary 0.5–0.75 whorl, filling less than 50% of digestive gland behind stomach, slightly overlapping posterior stomach chamber. Distal female genitalia shown in Figure 42F. Albumen gland having very short or no pallial component. Capsule gland shorter, narrower than albumen gland, ovate in section; rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a posterior-oblique loop preceded by small, posterior-oblique twist. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copulatrix slightly shorter than albumen gland, medium width, narrowly ovate, longitudinal, with 50% of length posterior to gland. Bursal duct originating from anterior edge at mid-line, very short, narrow-medium width. Seminal receptacle small, pouchlike, overlapping or ventral to anterior portion of bursa.

Testis 1.5 whorls, filling more than 50% of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland bean-shaped, pallial portion short, ovate in section. Proximal pallial vas deferens having well-developed, reflexed loop. Penis (Figure 42G–I) large; base rectangular, very weakly folded or smooth; filament short, narrow, tapering to point, oblique; lobe usually slightly longer than filament, knoblike or broadly triangular (tapering), strongly oblique. Terminal gland small, sub-circular, usually dorsal. Penial gland filling 25–50% of filament, narrow, positioned near inner edge. Dot-like gland positioned near outer edge medially (corresponding to Dg1) seen in one specimen. Ventral gland medium-sized, ovate, borne on prominent swelling, longitudinal, positioned alongside base of filament. Penial duct straight, near outer edge.

Type locality: Springs, East Fork Beaver Creek (above confluence of Cabin Creek), North Fork Humboldt River, Elko County, Nevada, T. 41 N, R. 57 E, SE ¼ section 27. Holotype, USNM 874722 (Figure 22H), collected by R. Hershler and P. Hovingh, 28 August, 1992; paratypes, USNM 860718. The type locality is a shallow, 8 m wide helocrene moderately impacted by cattle.

Remarks: This snail is contrasted with *P.* ***pictilis,*** from Antelope Valley (Lander County), above. *Pyrgulopsis* ***humboldtensis*** is also closely similar to some populations of widespread *P. kolobensis,* but differs in its broader shell, more pointed central cusps on the central radular teeth, more elongate outer wings on the lateral radular teeth, and smaller penial lobe with weaker terminal gland. The distribution of this species is shown in Figure 53.

Material examined: NEVADA. *Elko County:* Springs, East Fork Beaver Creek, T. 41 N, R. 57 E, SE ¼ section 27, USNM 860718, USNM 874722.—Springs, Hot Springs Creek, Marys River drainage, T. 39 N, R. 59 E, NW ¼ section 5, USNM 874725.—Springs, South Fork Hanks Creek, Marys River drainage, T. 40 N, R. 59 E, SW ¼ section 19, USNM 874719.—Spring, Marys River drainage, T. 39 N, R. 59 E, section 1, USNM 854544.

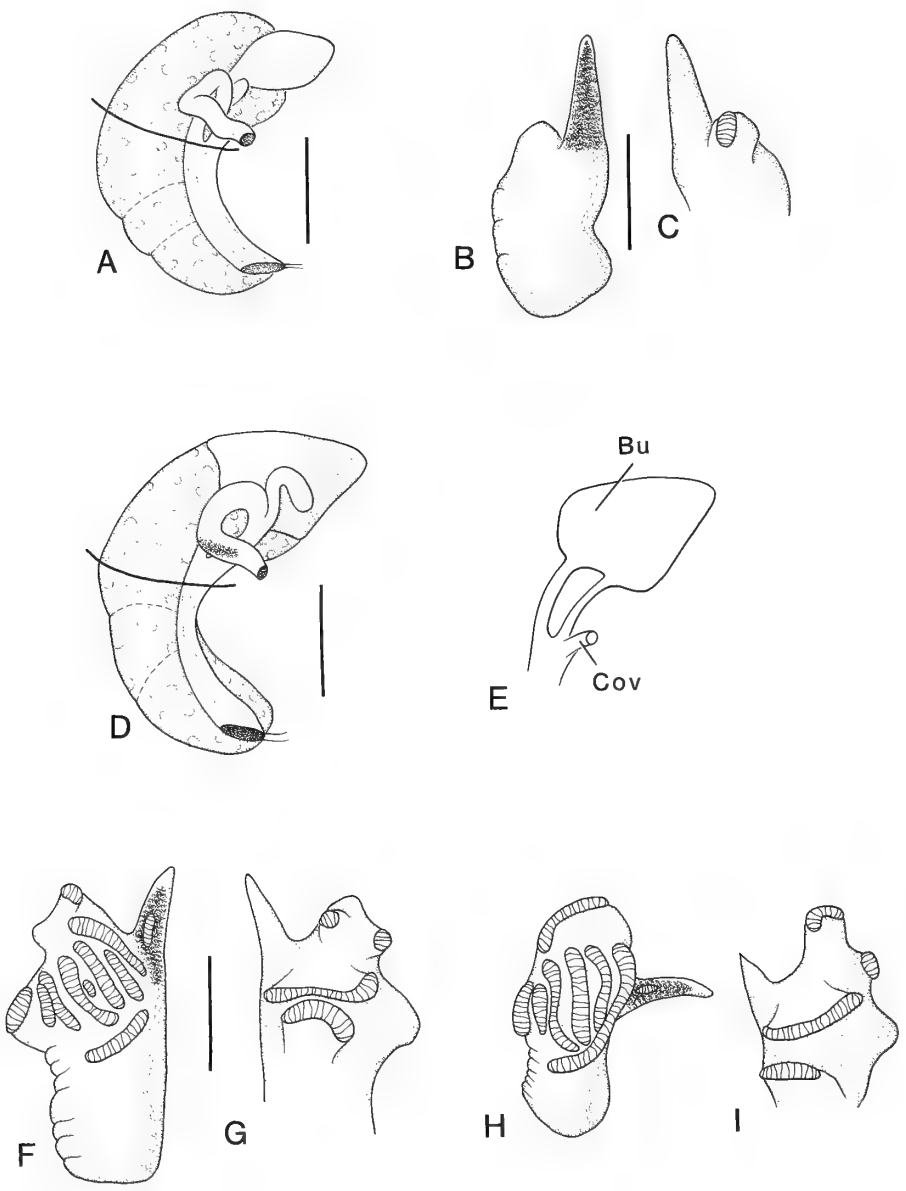


Figure 43

Genitalia of *Pyrgulopsis* species (A–C, *P.* ***hamlinensis,*** USNM 860695; D–G, *P.* ***peculiaris,*** USNM 883602; H, *P.* ***peculiaris,*** USNM 883603; I, *P.* ***peculiaris,*** USNM 874766). A. Female glandular oviduct and associated structures, bar = 0.25 mm. B. Dorsal aspect of penis, bar = 0.25 mm. C. Ventral aspect of distal penis, scale as in B. D. Female glandular oviduct and associated structures, bar = 0.25 mm. E. Bursa copulatrix and bifid duct, scale as in D. F. Dorsal aspect of penis, bar = 0.5 mm. G. Ventral aspect of distal penis, scale as in F. H. Dorsal aspect of penis, scale as in F. I. Ventral aspect of distal penis, scale as in F. A–E. Bars = 0.25 mm. F–I. Bars = 0.5 mm. Bu = bursa copulatrix, Cov = coiled oviduct.

Species from the Oregon Lakes

Pyrgulopsis hendersoni (Pilsbry, 1933)

Amnicola hendersoni Pilsbry, 1933, pl. 2: figs 2, 9, 10.
Fontelicella hendersoni (Pilsbry, 1933), Taylor, 1975:94–95 [literature compilation].
Fontelicella hendersoni (Pilsbry, 1933), Taylor & Smith, 1981:351–352 [locality records].
Pyrgulopsis hendersoni (Pilsbry, 1933), Hershler & Thompson, 1987:28–30 [transfer to *Pyrgulopsis*].—Hershler, 1994:39, 41 [figures].

Diagnosis: Large, with ovate to low-conical shell. Penis

large, filament short, lobe medium length. Penial ornament a large terminal gland, large Dg1, small Dg2, small Dg3, and small ventral gland.

Type locality: South of Burns, Oregon.

Remarks: The Abert Lake Basin population (Figure 53), although disjunct from the previously known range of *P. hendersoni* (Harney Lake and Malheur River basins to the northeast), closely conforms to this species, differing principally in having a smaller ventral gland on the penis. The large-snail collected by Taylor & Smith (1981:352; *F*[*ontelicella*]. sp.) from near the north end of Lake Abert also may be referable to this species.

Material examined: OREGON. *Lake County:* Springs, northwest corner Lake Abert, T. 33 S, R. 21 E, SW ¼ section 16, USNM 883547.

Pyrgulopsis intermedia (Tryon, 1865)

Pomatiopsis intermedia Tryon, 1865, 1865, pl. 22, fig. 8.
Fontelicella intermedia (Tryon, 1865), Taylor, 1975: 104 [literature compilation].—Taylor, 1985:308–310.
Pyrgulopsis intermedia (Tryon, 1865), Hershler & Thompson, 1987:28–30 [transfer to *Pyrgulopsis*].—Hershler, 1994:42, 44 [figures].

Diagnosis: Large, with ovate-conic shell. Penis medium-sized, filament and lobe medium length. Penial ornament a large terminal gland, medium-sized penial gland, and large ventral gland.

Type locality: Owyhee River, southeast Oregon.

Remarks: Taylor (1985) earlier noted on the occurrence of this snail in Barren Valley (Figure 53), a small endorheic drainage positioned between South Fork Malheur River and Owyhee River. Barren Valley populations closely resemble snails from the type locality area, but are slightly smaller and have squatter shells.

Material examined: OREGON. *Malheur County:* Skylight Spring, Barren Valley, T. 28 S, R. 38 E, SW ¼ section 8, USNM 854126.—Spring, Dowell Ranch, Barren Valley, T. 27 S, R. 38 E, SW ¼ section 33, USNM 874179.

Species from the Bonneville Basin

Pyrgulopsis kolobensis (Taylor, 1987)

Paludestrina longinqua (Gould, 1855), Pilsbry, 1899:122 [not Gould, 1855; in part].—Hannibal, 1912a:34 [in part].—Hannibal, 1912b:186 [in part].—Henderson & Daniels, 1916:322, 334 [in part].—Henderson & Daniels, 1917:64, 71, 72, 76.—Henderson, 1924:190.—Chamberlin & Jones, 1929:176–178, fig. 82 [in part].—Berry, 1931:114.—Jones, 1935:228 [in part?].—Jones, 1940a:42 [in part].—Jones, 1940b:29 [in part].—Woolstenhulme, 1942a:14 [in part].—Woolstenhulme, 1942b:55 [in part].
Amnicola (*Cincinnatia*) *cincinnatiensis* (Anthony, 1840), Henderson, 1924:190 [not Anthony, 1840].
Cincinnatia cincinnatiensis (Anthony, 1840), Chamberlin & Jones, 1929:175–176 [not Anthony, 1840].
Amnicola longinqua Gould, 1855, Call, 1884:20–21 [not Gould, 1855; in part].—Henderson, 1936:137 [in part].—Chamberlin & Roscoe, 1948:11.—E.G. Berry, 1948:69.
Fontelicella longinqua (Gould, 1855), Russell, 1971:232–233, fig. 4 (penis) [not Gould, 1855].
Fontelicella kolobensis Taylor, 1987:19, fig. 8.
Fontelicella pinetorum Taylor, 1987:20, fig. 9.—Hershler, 1994 [placed in synonymy with *Pyrgulopsis kolobensis*].
Pyrgulopsis kolobensis (Taylor, 1987), Hershler, 1994:44, 46 [figures; transfer to *Pyrgulopsis*].

Diagnosis: Medium-sized to large, shell usually ovate-conic. Penis large, filament short, lobe medium-long. Penial ornament variable, but typically a large terminal gland, small penial gland, and large ventral gland.

Type locality: Toquerville Springs, Washington County, Utah, T. 40 S, R. 13 W, section 35.

Remarks: This species (and its junior synonym, *Fontelicella pinetorum*) had been previously recorded only from the upper Virgin River basin in southwest Utah. However, *Pyrgulopsis kolobensis* is clearly conspecific with the widespread snail of the eastern Great Basin, which is found as far south as the northern flank of the mountain range composing the Great Basin-Virgin River divide, and which has been identified as *Paludestrina longinqua* Gould, 1855 in the literature. As explained elsewhere (Hershler, 1994:47), *Pyrgulopsis longinqua* (Gould, 1855) is restricted to its type locality area in the Salton Trough of southern California and, although these two species share some presumably derived penial features, they do not appear to be closely related (Hershler, 1994, fig. 31).

The range of *P. kolobensis* is herein extended to include much of the Bonneville Basin (including the Sevier River sub-basin and a few localities from both upper and lower Bear River drainage), as well as various isolated drainages of eastern Nevada and portions of the Colorado River basin (Meadow Valley Wash in southern Nevada, Strawberry River drainage in the Wasatch Mountains of Utah) (Figure 54).

Variation is considerable within this broadly distributed species. Although typically ovate-conic, the shell also may be either broadly conical (such as in populations from southern Steptoe Valley) or narrow-conic (Independence Valley). The terminal gland of the penis is usually fairly large and curved, but may also be short, and either ovate or (rarely) circular. The penial gland often is small (and is absent in one population from the Virgin River drainage) and confined to the base of the filament, but also may be long, filling most of the filament and often extending a short or long distance onto the base. In some populations the penial gland appears to be split and/or

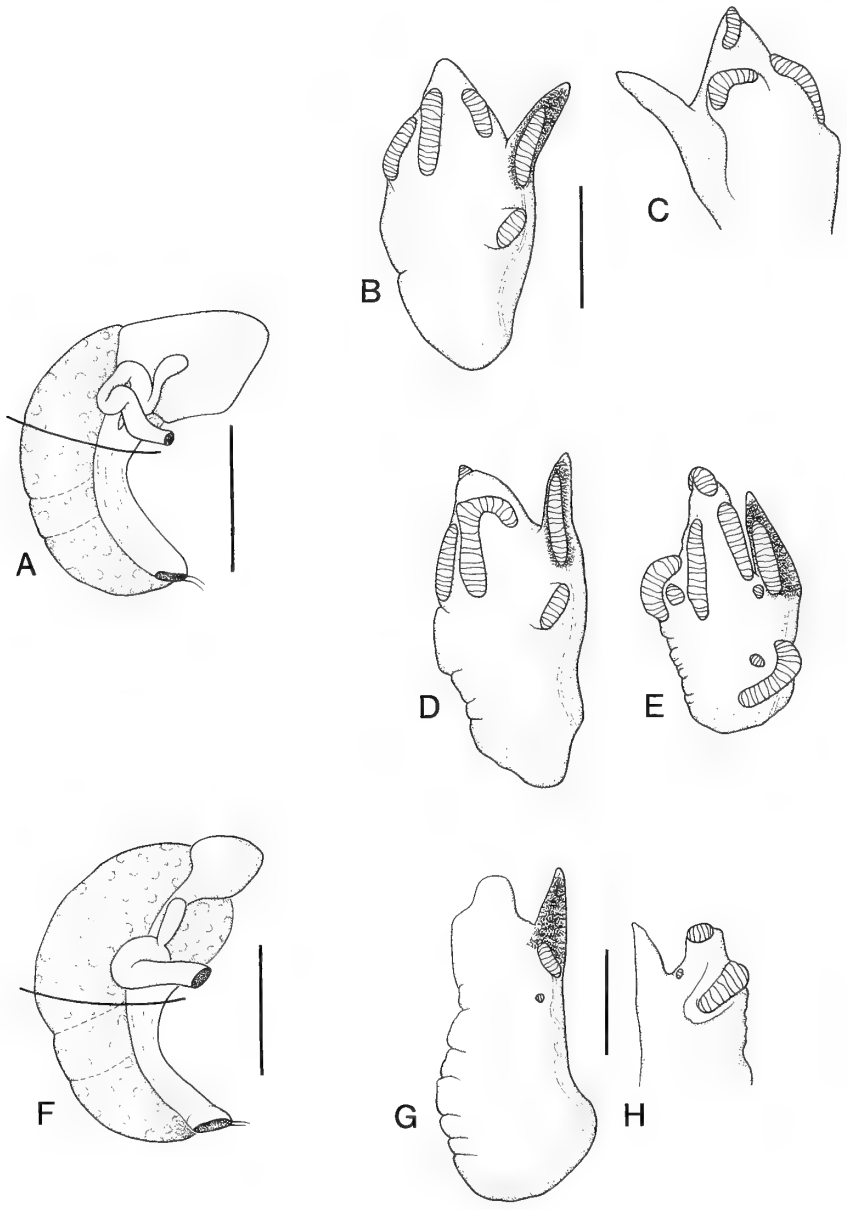


Figure 44

Genitalia of *Pyrgulopsis* species (A–E, *P. **anguina,*** USNM 860725; F–H, *P. **saxatilis,*** USNM 860726). A–E. Bars = 0.5 mm. F–H. Bars = 0.25 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis. Two sets of penes (B, C; D, E) are shown for *P. **anguina.***

accompanied by a more proximal, longitudinal Dg1. In many populations Dg1 is well developed, and may be raised on a pedicel and/or have a decidedly transverse orientation. A Dg2 often is present as a narrow, distal unit (sometimes raised). A proximal gland, also found along the inner edge, may also be present (notably in populations from Huntington, Newark, and Ruby Valleys), either instead of or in addition to the typical Dg2. In a few populations, the ventral gland is multiple (Mound Valley). Penial variation can be considerable even within a single population or among those of a small drainage and unusual forms are linked with typical morphology by intermediates in all cases, hence I choose not to sub-divide this taxon at this time.

Material examined: IDAHO. *Bannock County:* Heart

Mountain Spring (outflow), Stockton Creek, Bear River drainage, T. 13 S, R. 39 E, NW ¼ section 6, USNM 883681.—Spring, north of road along Stockton Creek, Bear River drainage, T. 13 S, R. 39 E, NW ¼ section 6, USNM 883691.—Stockton Creek, Bear River drainage, T. 13 S, R. 39 E, NW ¼ section 6, USNM 883536, USNM 883894. *Franklin County:* Spring, upper Cub River, Bear River drainage, T. 15 S, R. 41 E, NW ¼ section 8, USNM 874697, USNM 883568. *Oneida County:* Big Malad Spring, Malad Valley, T. 14 S, R. 35 E, NW ¼ section 10, USNM 883480.—Twin Springs, Curlew Valley, T. 13 S, R. 32 E, NW ¼ section 30, USNM 883595.—Springs, southeast of Stone Reservoir, Curlew Valley, T. 16 S, R. 33 E, NW ¼ section 7, USNM 883390. NEVADA. *Elko County:* Springs, north-northwest Denton Canyon, Butte Valley, T. 28 N, R. 62 E, SW ¼ section 3, USNM 874308.—Spring, north-northwest of The Narrows, Butte Valley, T. 28 N, R. 61 E, SW ¼ section 36, USNM 874283.—Springs, Toyn Creek, Mound Valley, T. 28 N, R. 57 E, SW ¼ section 5, USNM 874339.—Spring, Toyn Creek, Mound Valley, T. 28 N, R. 57 E, NW ¼ section 10, USNM 874257.—Spring, southwest side of North Sump, Ruby Valley, T. 27 N, R. 58 E, SW ¼ section 18, USNM 873337, USNM 874316.—Spring, southwest side of North Sump, Ruby Valley, T. 27 N, R. 58 E, section 7, USNM 873341.—Spring, southeast side of North Sump, Ruby Valley, T. 27 N, R. 58 E, SW ¼ section 10, USNM 873328, USNM 874282.—Spring, southeast side of North Sump, Ruby Valley, T. 27 N, R. 58 E, NE ¼ section 16, USNM 873338.—Gamble Spring, Thousand Springs Creek, T. 40 N, R. 69 E, NW ¼ section 8, USNM 874717.—Hellman Spring, Huntington Valley, T. 27 N, R. 55 E, NE ¼ section 36, USNM 874078, USNM 874337.—Springs, South Fork Twin Creek, Huntington Valley, T. 27 N, R. 56 E, SE ¼ section 6, USNM 874071, USNM 874317, USNM 874674.—Big Springs, Independence Valley, T. 36 N, R. 66 E, NE ¼ section 33, USNM 874330. *Eureka County:* upper Huntington Creek, Huntington Valley, T. 25 N, R. 55 E, NW ¼ section 35, USNM 874333.—upper Huntington Creek, Huntington Valley, T. 25 N, R. 55 E, SE ¼ section 34, USNM 873336.—Spring, upper Huntington Creek, Huntington Valley, T. 25 N, R. 55 E, SE ¼ section 34, USNM 873410.—Fish Creek Springs, Fish Creek Valley, T. 16 N, R. 53 E, NW ¼ section 8, USNM 874764, USNM 874875.—Simpson Springs, Diamond Valley, T. 19 N, R. 54 E, NW ¼ section 22, USNM 874324.—Springs, Roberts Creek, Kobeh Valley, T. 23 N, R. 50 E, NE ¼ section 35, USNM 874334.—Pratt Springs, Pine Valley, T. 27 N, R. 52 E, SE ¼ section 10, USNM 874301.—Tonkin Spring, Denay Valley, T. 23½ N, R. 49 E, SW ¼ section 1, USNM 874313, USNM 874716.—Hand-Me-Down Creek, Crescent Valley, T. 28 N, R. 49 E, SE ¼ section 3, USNM 874302. *Lincoln County:* Spring, Kershaw-Ryan State Park, Meadow Valley Wash, T. 4 S, R. 67 E, NE ¼ section 19, USNM 854170, USNM 873184, USNM 873455, USNM 874039, USNM 874761.—North Spring, Clover Valley, Meadow Valley Wash, T. 5 S, R. 69 E, SW ¼ section 11, USNM 874768.—Spring, Spring Valley State Park, Meadow Valley Wash, T. 2 N, R. 70 E, NE ¼ section 7, USNM 874675, USNM 874777.—Spring, west-northwest of Cottonwood Wash, Spring Valley, Meadow Valley Wash, T. 2 N, R. 70 E, NW ¼ section 5, USNM 874679, USNM 874766. *Nye County:* Butterfield Springs, White River Valley, T. 7 N, R. 57 E, NE ¼ section 28, USNM 873155.—Springs below Black Spring, Sand Creek, Garden Valley, T. 3 N, R. 57 E, NW ¼ section 27, USNM 874661.—Butterfield Springs, Railroad Valley, T. 8 N, R. 57 E, SE ¼ section 27, USNM 873155.—Thorn Spring (north), Railroad Valley, T. 7 N, R. 57 E, SW ¼ section 28, USNM 883854.—Thorn Spring, Railroad Valley, T. 7 N, R. 57 E, section 28, USNM 874087.—Spring, Troy Canyon, Railroad Valley, T. 6 N, R. 57 E, SW ¼ section 28, USNM 883845.—Stream, Troy Canyon, Railroad Valley, T. 6 N, R. 57 E, NE ¼ section 34, USNM 883247.—Spring, northeast of Tom Spring, Railroad Valley, T. 8 N, R. 57 E, SW ¼ section 1, USNM 873169.—Springs, ca. 2.4 km north-northwest of Currant, Railroad Valley, T. 11 N, R. 58 E, NW ¼ section 32, USNM 873171.—Spring, south of Cottonwood Canyon, Reveille Valley, T. 2 N, R. 50 E, NE ¼ section 28, USNM 883546. *White Pine County:* Spring, Snake Creek, Snake Valley, T. 12 N, R. 70 E, NW ¼ section 17, USNM 874670.—Spring, Snake Creek, Snake Valley, T. 12 N, R. 70 E, section 16, USNM 873430.—Willow Patch Spring, Snake Valley, T. 15 N, R. 68 E, SE ¼ section 36, USNM 854169, USNM 874281, USNM 874669.—Spring, southwest of Caine Spring, Snake Valley, T. 15 N, R. 17 E, NE ¼ section 31, USNM 874277.—Spring, Minerva, Spring Valley, T. 11 N, R. 67 E, SE ¼ section 12, USNM 874668.—Spring, 1.6 km north of Minerva, Spring Valley, T. 11 N, R. 67 E, SW ¼ section 1, USNM 874665.—Spring, 3.2 km north of Minerva, Spring Valley, T. 12 N, R. 67 E, NW ¼ section 36, USNM 873217, USNM 874676.—Springs, southeast of Cleve Creek, Spring Valley, T. 16 N, R. 67 E, SW ¼ section 32, USNM 874332.—Springs, southeast of Cleve Creek, Spring Valley, T. 16 N, R. 67 E, NE section 32, USNM 873229.—Springs, southeast of Cleve Creek (0.3 km east of above), Spring Valley, T. 16 N, R. 67 E, NE section 32, USNM 873199.—Spring, lower Cleve Creek, Spring Valley, T. 16 N, R. 67 E, SW ¼ section 20, USNM 873225.—Springs, Stonehouse, Spring Valley, T. 22 N, R. 66 E, SW ¼ section 17, USNM 874309.—Cane Spring, Pleasant Valley, T. 21 N, R. 70 E, SW ¼ section 22, USNM 874279.—Lower Sanford Spring, Deep Creek Valley, T. 23 N, R. 69 E, NE ¼ section 25, USNM 874274.—Springs, West Deep Creek, Deep Creek Valley, T. 24 N, R. 70 E, NE ¼ section 3, USNM 874278.—Tippett Springs, Antelope Valley, T. 23 N, R. 67 E, NW ¼ section 14, USNM 874338, USNM 883592.—Chin Creek, Antelope Valley, T. 25 N, R. 67 E, NE ¼ section

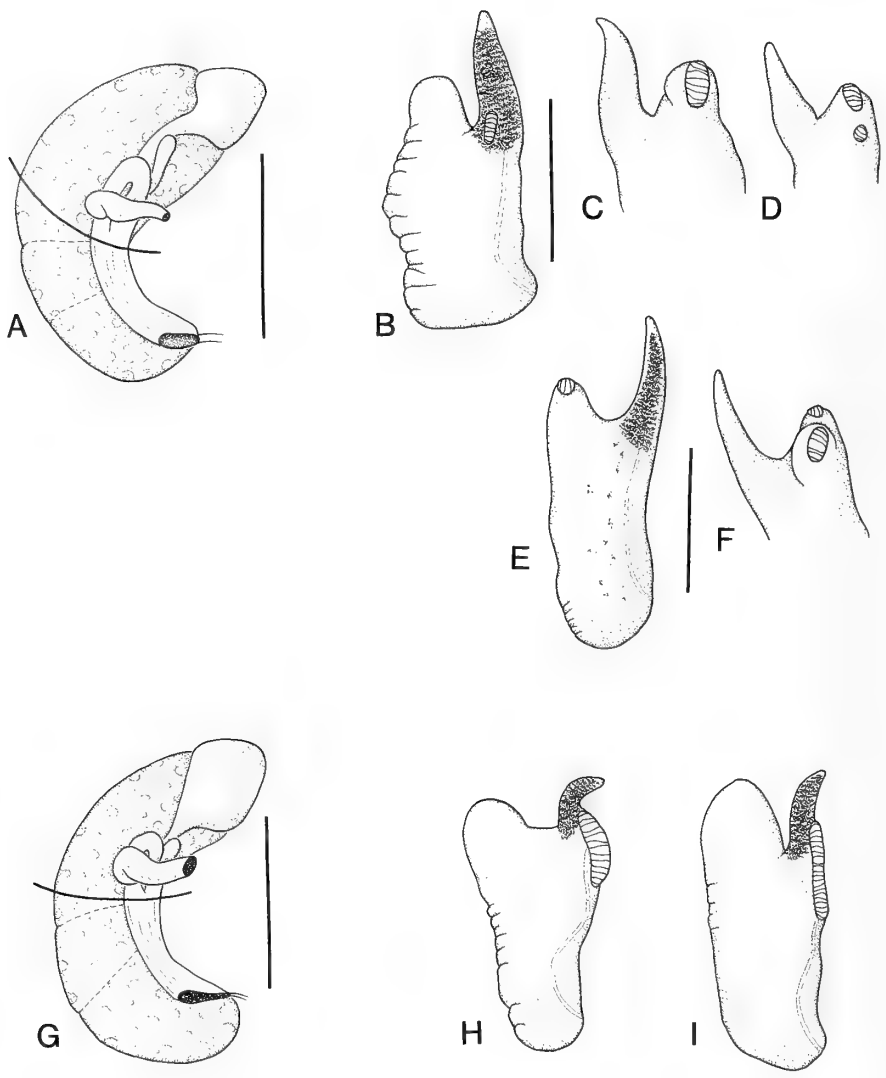


Figure 45

Genitalia of *Pyrgulopsis* species (A–D, *P.* ***variegata,*** USNM 860723; E, F, *P.* ***variegata,*** USNM 883599; G–I, *P.* ***hovinghi,*** USNM 874715). Bars = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis (not shown for *P.* ***hovinghi,*** which lacks ventral ornament). Two sets of penes (B, C; E, F) and a third example of the ventral penis (D) are shown for *P.* ***variegata.***

26, USNM 874323.—Spring, west side HWY 318, ca. 9.6 km south of Lund, White River Valley, T. 11 N, R. 62 E, USNM 873161.—Spring, west side HWY 6, west-northwest of Preston, White River Valley, T. 13 N, R. 61 E, SW ¼ section 31, USNM 873330, USNM 874680.—Spring, Bull Creek, Railroad Valley, T. 14 N, R. 56 E, SE ¼ section 14, USNM 874774, USNM 874881.—Green Springs, Railroad Valley, T. 15 N, R. 57 E, SW ¼ section 33, USNM 874773, USNM 874874.—Bennett Spring, Steptoe Valley, T. 19 N, R. 63 E, SE ¼ section 33, USNM 874303.—Springs, northwest of Clark Spring, Steptoe Valley, T. 19 N, R. 63 E, NE ¼ section 32, USNM 873220.—Springs, northwest of Clark Spring, Steptoe Valley, T. 19 N, R. 63 E, NW ¼ section 20, USNM 874691, USNM 883937.—Springs, Steptoe Ranch, Steptoe Valley, White Pine County, Nevada, T. 19 N, R. 63 E, SW ¼ section 5, USNM 892017.—Springs, Steptoe Ranch, Steptoe Valley, T. 19 N, R. 63 E, NW ¼ section 5, USNM 873221.—Spring, north of Steptoe Ranch, Steptoe Valley, White Pine County, Nevada, T. 19 N, R. 63 E, SW ¼ section 5, USNM 873206.—Spring, Schell Creek, Steptoe Valley, T. 22 N, R. 65 E, NE ¼ section 7,

USNM 874325.—Springs, Schell Creek, ca. 1 km below Schellbourne Pass, Steptoe Valley, T. 22 N, R. 65 E, SE ¼ section 5, USNM 873236.—Owens Springs, Butte Valley, T. 26 N, R. 62 E, NW ¼ section 33, USNM 874321.—Springs, southwest side of Newark Lake, Newark Valley, T. 20 N, R. 55 E, sections 4, 5, 8, USNM 873332.—Minoletti Spring, Newark Valley, T. 22 N, R. 55 E, NW ¼ section 11, USNM 874328.—Cold Spring, Newark Valley, T. 23 N, R. 55 E, NW ¼ section 26, USNM 874320, USNM 874901.—Station Spring, Ruby Valley, T. 25 N, R. 57 E, NE ¼ section 13, USNM 874311.—Narcise Springs, Ruby Valley, T. 25 N, R. 57 E, SW ¼ section 2, USNM 874307.—Springs, northwest of Narcise Springs, Ruby Valley, T. 25 N, R. 57 E, NE ¼ section 3, USNM 873335. UTAH. *Box Elder County:* Blue Creek Spring, Blue Creek Valley, T. 13 N, R. 5 W, NW ¼ section 29, USNM 883625.—Spring, ca. 3.5 km east-northeast of Portage, Malad Valley, T. 15 N, R. 3 W, NE ¼ section 4, USNM 883490, USNM 883577.—Spring, ca. 1.6 km north of Promonotory Point, Promontory Mountains, Great Salt Lake Desert, T. 6 N, R. 5 W, NE ¼ section 21, USNM 883611.—Shaw Spring, Promontory Mountains, Great Salt Lake Desert, T. 7 N, R. 5 W, NE ¼ section 9, USNM 883607.—Springs, ca. 1.6 km south of Sweetwater Spring, Promontory Mountains, Great Salt Lake Desert, T. 8 N, R. 5 W, center section 5, USNM 883632.—Spring, east of Rozel Flat, Promontory Mountains, Great Salt Lake Desert, T. 9 N, R. 6 W, NE ¼ section 31, USNM 854782.—Spring, ca. 0.8 km north of Mantua Reservoir, Great Salt Lake Desert, T. 9 N, R. 1 W, NE ¼ section 16, USNM 883569.—Salt Spring, Point Lookout, Salt Creek, Great Salt Lake Desert (Figure 5C), T. 11 N, R. 3 W, SE ¼ section 6, USNM 874067, USNM 883216.—Spring, Painted Rock, Salt Creek, Great Salt Lake Desert, T. 10 N, R. 4 W, NW ¼ section 11, USNM 883209, USNM 883399.—Spring, Jesses Knoll, Salt Creek, Great Salt Lake Desert, T. 11 N, R. 4 W, SE ¼ section 34, USNM 874069, USNM 883234, USNM 883400.—Springs, west-southwest of Connor Springs, Salt Creek, Great Salt Lake Desert, T. 10 N, R. 5 W, NW ¼ section 12, USNM 883198, USNM 883401.—Spring, southwest of Lampo Junction, Great Salt Lake Desert, T. 10 N, R. 5 W, NE ¼ section 4, USNM 854548, USNM 883388.—Bar M Spring, Great Salt Lake Desert (Figure 5B), T. 11 N, R. 10 W, SE ¼ section 1, USNM 883630.—Spring, east side HWY 30, west of Dove Creek Hills, Great Salt Lake Desert, T. 11 N, R. 15 W, NW ¼ section 14, USNM 883615.—So. Tremonton, FMNH 178357.—Spring, north of Plymouth, Malad Valley, FMNH 224314. *Cache County:* Spring, below (west of) Porcupine Reservoir, Cache Valley, T. 9 N, R. 2 E, NW ¼ section 17, USNM 883853.—Pool alongside Logan River, Logan Canyon, Cache Valley, T. 12 N, R. 2 E, NW ¼ section 27, USNM 883575.—Spring, Spring Hollow, Logan Canyon, Cache Valley, T. 12 N, R. 2 E, NW ¼ section 27, USNM 858290.—Murray Spring; Cache Valley, T. 10 N, R. 1 W, SW ¼ section 10, USNM 883476. *Davis County:* Spring, ca. 1.6 km northeast of Mushroom Spring, Antelope Island, Great Salt Lake Desert, T. 2 N, R. 3 W, NW ¼ section 11, USNM 883219, USNM 883489. *Iron County:* Spring, east of Summit, Parowan Valley, T. 34 S, R. 9 W, SE ¼ section 31, USNM 883612.—Spring, upper Little Creek, Parowan Valley, T. 34 S, R. 7 W, NE ¼ section 17, USNM 883616.—Kane Spring, Parowan Valley, T. 32 S, R. 9 W, NE ¼ section 12, USNM 883593.—Spring, Upper Bear Valley, T. 33 S, R. 7 W, NE ¼ section 23, USNM 883619.—West Spring, Lower Bear Valley, T. 32 S, R. 6 W, SW ¼ section 28, USNM 883589.—Big Swamp Springs, Lower Bear Valley, T. 32 S, R. 6 W, NW ¼ section 23, USNM 883601. *Juab County:* Springs, McIntyre, Tintic Valley, T. 11 S, R. 3 W, SE ¼ section 28, USNM 883206.—Baker Hot Springs, Old River Bed, T. 14 S, R. 8 W, SE ¼ section 10, USNM 883238, USNM 883431.—Cherry Creek, below Indian Springs, Old River Bed, T. 12 S, R. 5 W, NW ¼ section 21, USNM 883197.—Spring, Mount Laird, Sevier Desert, T. 14 S, R. 11 W, center section 26, USNM 883226, USNM 883432.—Spring, northeast of Chicken Creek Reservoir, Juab Valley, T. 15 S, R. 1 W, NE ¼ section 16, USNM 883426, USNM 883438.—Springs, Hollow Creek, Juab Valley, T. 13 S, R. 2 E, NW ¼ section 5, USNM 883600.—Springs, Curiant Creek, Juab Valley, T. 12 S, R. 1 E, NW ¼ section 18, USNM 883195.—Spring, Mona, Juab Valley, T. 11 S, R. 1 E, NE ¼ section 31, USNM 874077, USNM 883240.—Spring, south of Starr, Juab Valley, T. 11 S, R. 1 E, SW ¼ section 8, USNM 874070, USNM 874072, USNM 883231.—"Percy Spring," south end Fish Springs National Wildlife Refuge, Great Salt Lake Desert, T. 11 S, R. 14 W, SE ¼ section 26, USNM 858289, USNM 883473.—Spring, near south end Fish Springs National Wildlife Refuge, Great Salt Lake Desert, T. 11 S, R. 14 W, NE ¼ section 26, USNM 858280.—Spring, southwest of "Mallard Pool," Fish Springs National Wildlife Refuge, Great Salt Lake Desert, T. 11 S, R. 14 W, NE ¼ section 23, USNM 883200.—North Springs, Fish Springs National Wildlife Refuge, Great Salt Lake Desert, T. 11 S, R. 14 W, SE ¼ section 3, USNM 883217.—"Leland Harris" Springs, Snake Valley, T. 14 S, R. 18 W, NE ¼ section 32, USNM 883223.—Spring (source), Spring Creek, Deep Creek Valley, T. 11 S, R. 19 W, SW ¼ section 19, USNM 874276. *Millard County:* Coyote Spring, Beaver River drainage, T. 23 S, R. 9 W, NW ¼ section 33, USNM 883239.—Tie House Spring, Beaver River drainage, T. 24 S, R. 10 W, NE ¼ section 22, USNM 883212.—Spring Lake (Clear Lake), Sevier River drainage, T. 20 S, R. 7 W, NW ¼ section 11, USNM 883214.—Painter Spring, Tule Valley, T. 19 S, R. 14 W, NE ¼ section 5, USNM 883202.—Sinbad Spring, Tule Valley, T. 16 S, R. 13 W, NE ¼ section 33, USNM 883207, USNM 883424.—Spring, at corral, east of Horse Canyon, Snake Valley, T. 17 S, R. 19 W, NE ¼ section 29, USNM 883220.—Knoll

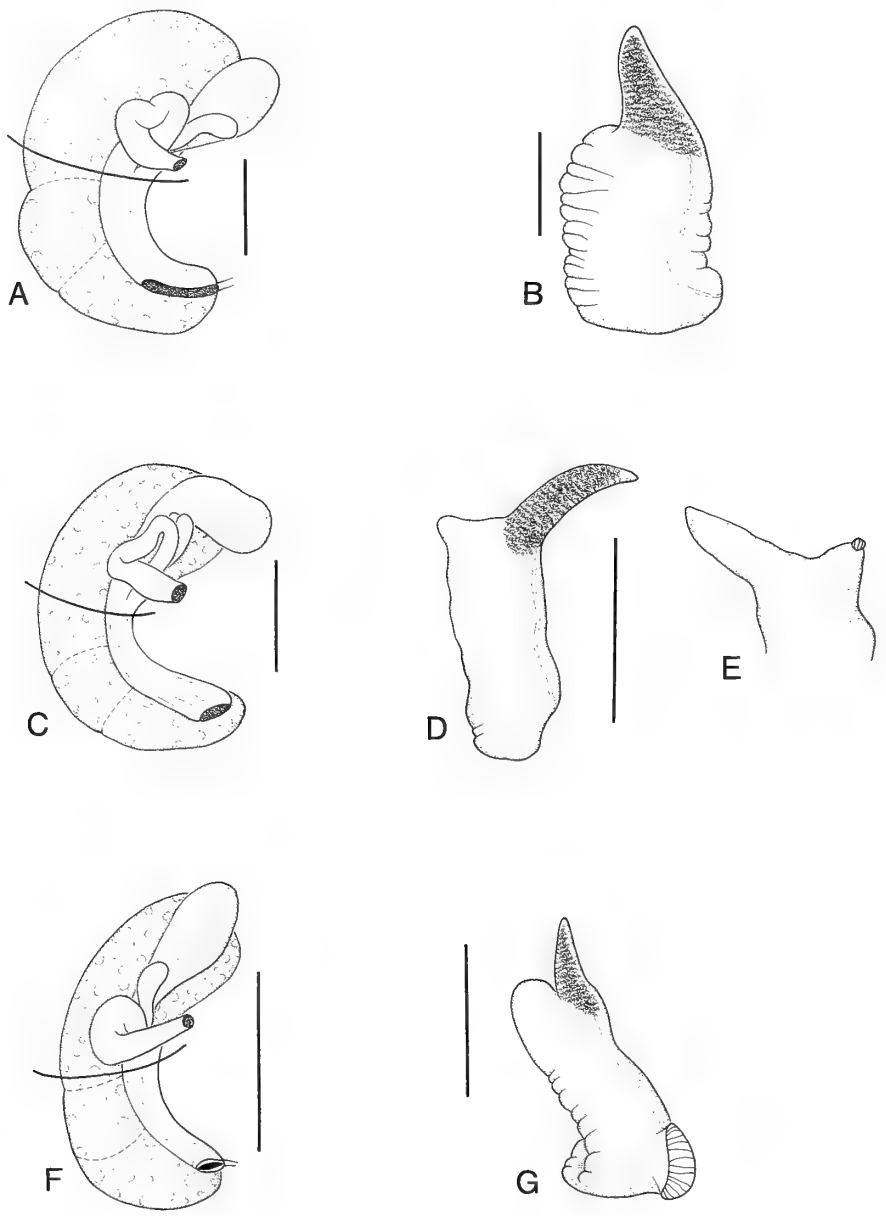


Figure 46

Genitalia of *Pyrgulopsis* species (A, B, *P.* ***millenaria,*** USNM 860721; C–E, *P.* ***lentiglans,*** USNM 860722; F, G, *P.* ***plicata,*** USNM 860727). A, B, Bars = 0.25 mm. C–G. Bars = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis (not shown for *P.* ***millenaria*** and *P.* ***lentiglans,*** which lack ventral ornament).

Springs, Snake Valley, T. 18 S, R. 18 W, NE ¼ section 16, USNM 883218.—Twin Springs, Snake Valley, T. 16 S, R. 18 W, SW ¼ section 22, USNM 883208.—Cold Spring, Snake Valley, T. 16 S, R. 19 W, NW ¼ section 2, USNM 883213. *Morgan County:* Spring, East Canyon, Weber River drainage, T. 1 N, R. 3 E, NW ¼ section 14, USNM 883389.—Spring, East Canyon, Weber River drainage, T. 1 N, R. 3 E, SE ¼ section 15, USNM 874074.—Dixie Spring, East Canyon Creek, Weber River drainage, T. 2 N, R. 3 E, NE ¼ section 1, USNM 883634.—Lost Creek near Devils Slide, Weber River drainage, T. 4 N, R. 4 E, SE ¼ section 19, USNM 883596.—Devils Slide, FMNH 179260, FMNH 179307. *Rich County:* Spring, lower Home Canyon, Bear River drainage, T. 8 N, R. 6 E, SW ¼ section 24, USNM 883485. *Salt Lake County:* Spring, Riverton, Jordan River

drainage, T. 3 S, R. 1 W, NW ¼ section 34, USNM 883236, USNM 883284.—Spring, HWY 80, Parleys Canyon (just below Parleys Summit), Jordan River drainage, T. 1 S, R. 3 E, SE ¼ section 8, USNM 858287, USNM 883628.—Spring, Emigration Canyon (near mouth), Jordan River drainage, T. 1 S, R. 1 E, NE ¼ section 11, USNM 883613.—Spring, (upper) City Creek Canyon, Jordan River drainage, T. 1 N, R. 1 E, NW ¼ section 13, USNM 883606.—Spring, City Creek Canyon, Jordan River drainage, T. 1 N, R. 1 E, section 30, USNM 874073, USNM 874374, USNM 874375, USNM 883588.—Spring, City Creek Canyon, USNM 31271.—Lambs Canyon, Great Salt Lake Desert, FMNH 178387.—Mill Creek Canyon, Jordan River drainage, FMNH 178363.—Liberty Park, Salt Lake City, FMNH 178516.—south Salt Lake City, FMNH 179664.—33rd and 7th Street E, Salt Lake City, FMNH 178372.—Emigration Canyon, Great Salt Lake Desert, FMNH 178444.—City Creek, Salt Lake City, FMNH 178874, FMNH 178392.—City Creek, north bridge, FMNH 178362.—Red Butte Canyon, Great Salt Lake Desert, FMNH 178368, FMNH 178384.—Red Butte, Great Salt Lake Desert, FMNH 178369.—Tarpeys Spring, Salt Lake City, USNM 199398.—Salt Lake City, USNM 414181, USNM 424340.—Clintons Cave (sub-fossil), FMNH 178385, FMNH 223987, FMNH 224407. *Sevier County:* Springs, Live Oak Canyon, Sevier River drainage, T. 26 S, R. 3 W, NW ¼ section 4, USNM 883581.—Spring, 2.2 km south of Sigurd, Sevier River drainage, T. 23 S, R. 2 W, NW ¼ section 12, USNM 883428, USNM 883934. *Summit County:* Spring, southwest of Francis, Provo River drainage, T. 2 S, R. 6 E, SE ¼ section 32, USNM 883620.—Spring, Peoa, Weber River drainage, T. 1 S, R. 5 E, section 23, USNM 874384.—Spring, Peoa, Weber River drainage, T. 1 S, R. 5 E, section 23, USNM 874076.—Spring, Peoa, Weber River drainage, T. 1 S, R. 5 E, SE ¼ section 14, USNM 883629.—Beard Spring, Weber River drainage, T. 3 N, R. 4 E, SE ¼ section 19, USNM 883580. *Tooele County:* Springs, Dog Hollow Creek, Rush Valley, T. 9 S, R. 4 W, SE ¼ section 20, USNM 883196.—Spring, south end Atherly Reservoir, Rush Valley, T. 7 S, R. 5 W, SW ¼ section 28, USNM 883488.—Springs, south of Rush Lake, Rush Valley, T. 5 S, R. 5 W, NW ¼ section 2, USNM 883483.—Spring, below Little Pole Canyon, Skull Valley, T. 3 S, R. 7 W, SW ¼ section 30, USNM 883626.—Springs (southernmost), west of Salt Mountain, Skull Valley, T. 3 S, R. 8 W, SW ¼ section 16, USNM 883233.—Horseshoe Springs, Skull Valley, T. 2 S, R. 8 W, SE ¼ section 26, USNM 858285, USNM 873436, USNM 883204.—Muskrat Spring, Skull Valley, T. 2 S, R. 8 W, UMMZ 219484.—Big Spring, Skull Valley, T. 1 S, R. 7 W, SE ¼ section 8, USNM 858282, USNM 883199, USNM 883282.—Spring, northwest of Flux, Tooele Valley, T. 1 S, R. 7 W, NE ¼ section 25, USNM 883225, USNM 883398.—Spring, Lake Point, Tooele Valley, T. 1 S, R. 4 W, SE ¼ section 24, USNM 883621.—Near Lake Point, Tooele Valley, USNM 47864.—"Redden Springs," ca. 9.6 km north of Callao, Great Salt Lake Desert, T. 9 S, R. 16 W, SW ¼ section 31, USNM 883203.—Blue Lake, Great Salt Lake Desert, T. 4 S, R. 19 W, SW ¼ section 6, USNM 883232.—Spring feeding Blue Lake, Great Salt Lake Desert, T. 4 S, R. 19 W, SE ¼ section 6, USNM 883224, USNM 883633.—Stream, 3.2 km west of Bonneville Service Station, near Timpi (Timpie), FMNH 178400 (mixed with *Tryonia protea* [Gould, 1855]).—West side of Skull Valley (subfossil), FMNH 178423.—4.8 km south of Stockton, Rush Valley, FMNH 178380.—Spring before Josepha, Skull Valley, FMNH 178382 (mixed with *Tryonia protea*).—First spring south of Josepha, Skull Valley, FMNH 178381.—Southeast of Tooele, FMNH 224405. *Utah County:* Springs, Warm Springs Ditch, Goshen Valley (Utah Lake Basin), T. 10 S, R. 1 E, center section 8, USNM 883230.—Holladay Springs, Utah Lake Basin, T. 9 S, R. 1 E, NE ¼ section 25, USNM 883605.—Spring, Right Fork Hobble Creek, Utah Lake Basin, T. 7 S, R. 4 E, SW ¼ section 24, USNM 883570.—"Clyde Spring," Hobble Creek, Utah Lake Basin, T. 8 S, R. 3 E, SE ¼ section 3, USNM 883935.—Spring, Diamond Fork, Utah Lake Basin, T. 8 S, R. 5 E, NE ¼ section 32, USNM 873331, USNM 883571.—Spring, South Fork Provo River, T. 5 S, R. 3 E, NE ¼ section 36, USNM 883609.—Spring (source), Spring Creek, below Mill Pond, Utah Lake Basin, T. 5 S, R. 1 E, SW ¼ section 15, USNM 883229, USNM 883285.—Big Spring, west of Fairfield, Cedar Valley, T. 6 S, R. 2 W, SE ¼ section 30, USNM 883235.—Spring, Cedar Fort, Cedar Valley, T. 6 S, R. 2 W, SW ¼ section 6, USNM 883281, USNM 883429.—Spanish Fork Canyon (sixth water canyon), FMNH 178370, FMNH 178376. *Wasatch County:* Spring, Willow Creek, Strawberry River drainage (Colorado River drainage basin), T. 6 S, R. 12 W, SE ¼ section 14, USNM 883617.—Spring Creek, Wallsburg, Provo River drainage, T. 5 S, R. 5 E, ¼ section 18, USNM 883618.—Cascade Springs, Provo River drainage, T. 4 S, R. 3 E, NE ¼ section 24, USNM 873339, USNM 883635.—Spring, along HWY 40–189, ca. 2.0 km north Heber City, Heber Valley, Provo River drainage, T. 3 S, R. 5 E, SW ¼ section 29, USNM 883623.—Hot Springs, northwest of Midway, Heber Valley, Provo River drainage, T. 3 S, R. 4 E, SW ¼ section 27, USNM 883794, USNM 883844.—Spring, east of Hailstone, Provo River drainage, T. 2 S, R. 5 E, NE ¼ section 33, USNM 874372.—Spring, east of Hailstone, Provo River drainage, T. 2 S, R. 5 E, SE ¼ section 33, USNM 873340.—Drain Tunnel Creek, Provo River drainage, T. 2 S, R. 5 E, NE ¼ section 19, USNM 858284.—Drain Tunnel Creek, Provo River drainage, T. 2 S, R. 5 E, SE ¼ section 19, USNM 873334.—Ross Creek, Provo River drainage, T. 2 S, R. 5 E, NE ¼ section 18, USNM 883631.—Provo River, below Charleston, FMNH 179177. *Washington County:* Springs, west side Left Fork

of North Creek, Virgin River drainage, T. 40 S, R. 11 W, NE ¼ section 28, USNM 847248.—Leeds, Virgin River drainage, FMNH 178356.—Springs, Left Fork Santa Clara River, Pine Valley, T. 39 S, R. 14 W, SW ¼ section 20, USNM 847029, USNM 883258.—Spring, Pinto Creek, Escalante Desert, T. 38 S, R. 15 W, NE ¼ section 12, USNM 874735.—Pinto Spring, Escalante Desert, T. 38 S, R. 14 W, center section 6, USNM 883211.—Spring, southwest of Pinto, Pinto Creek, Escalante Desert, T. 37 S, R. 15 W, SE ¼ section 33, USNM 883228.—Springs, Calf Springs Creek, Escalante Desert, T. 38 S, R. 17 W, NE ¼ section 4, USNM 883201. *Weber County:* Spring, mouth of Ogden County, Ogden River drainage, T. 6 N, R. 1 W, SW ¼ section 23, USNM 883598.—Springs, North Fork Ogden River, T. 7 N, R. 1 E, NE ¼ section 18, USNM 883604.

Pyrgulopsis pilsbryana (Baily & Baily, 1952)

Amnicola pilsbryi Baily & Baily, 1951:50, pl. 4, fig. 3 [not *Amnicola pilsbryi* Walker, 1906].
Amnicola pilsbryana Baily & Baily, 1952:144 [new name for *Amnicola pilsbryi* Baily & Baily, 1951].
Fontelicella pilsbryana (Baily & Baily, 1952), Taylor, 1975: 152 [literature compilation].
Fontelicella pilsbryi (Baily and Baily, 1951), Taylor, 1975: 153 [literature compilation].
Pyrgulopsis pilsbryana (Baily & Baily, 1952), Hershler and Thompson, 1987:28–30 [transfer to *Pyrgulopsis*].—Hershler, 1994:60 [figures].

Diagnosis: Medium-sized to large, with ovate- to narrow-conic shell. Penis large, filament and lobe medium length. Penial ornament a medium-sized terminal gland, very small-large penial gland, and minute Dg3.

Type locality: Lifton, Ideal Beach, Bear Lake, Idaho.

Remarks: The range of this species (previously restricted to the type locality area in Bear Lake basin) encompasses the Bear Lake basin and Bear River basin, both above and below (above Cache Valley) the Bear Lake outlet (Figure 55). The distribution of this species closely abuts that of *P. kolobensis,* a similar species which differs in having a ventral gland on the penis. Populations of *P. pilsbryana* vary principally in terms of shell shape and length of penial gland.

Material examined: IDAHO. *Bear Lake County:* Spring, St. Charles Canyon, Bear Lake Basin, T. 15 S, R. 43 E, SE ¼ section 17, USNM 858281, USNM 883444.—Spring, northeast side Merkley Lake, Bear Lake drainage, T. 14 S, R. 44 E, NE ¼ section 26, USNM 883585.—Spring, Stauffer Creek, Bear River drainage, T. 11 S, R. 43 E, NE ¼ section 27, USNM 883587. *Caribou County:* Ledger Creek, Soda Springs, Bear River drainage, T. 9 S, R. 42 E, SE ¼ section 5, USNM 883537, USNM 883895.—Pond outflow, Kelly Park, Soda Springs, Bear River drainage, T. 9 S, R. 42 E, NW ¼ section 5, USNM 883534, USNM 883535, USNM 883889.—Formation Spring, Bear River drainage, T. 8 S, R. 42 E, section 28, USNM 874153.—Formation Spring (outflow), Bear River drainage, T. 8 S, R. 42 E, SE ¼ section 28, USNM 883567.—Kackley Spring, Gem Valley, Bear River drainage, T. 10 S, R. 40 E, SW ¼ section 21, USNM 883538, USNM 883891.—Spring (source), Whiskey Creek, Gentile Valley, Bear River drainage, T. 11 S, R. 41 E, SE ¼ section 7, USNM 883441. *Franklin County:* Spring Creek, HWY 34 crossing, Mound Valley, Bear River drainage, T. 12 S, R. 41 E, NW ¼ section 18, USNM 883423. UTAH. *Rich County:* Jacobsen Springs, Big Creek, Bear River drainage, T. 10 N, R. 6 E, SW ¼ section 1, USNM 883578.—Big Spring, Bear Lake Basin, T. 12 N, R. 5 E, NE ¼ section 4, USNM 883586.—Spring, ca. 0.8 km north of Lakota, Bear Lake Basin, T. 15 N, R. 5 E, SE ¼ section 32, USNM 883574. WYOMING. *Lincoln County:* Springs, Bear River drainage, T. 22 N, R. 120 W, section 26, USNM 883896.

Pyrgulopsis ***hamlinensis*** Hershler, sp. nov.

Hamlin Valley pyrg
(Figures 9I, 22K, 43A–C)

Etymology: Referring to endemism of this snail in Hamlin Valley, Utah.

Diagnosis: Small, with narrow-conic shell. Penis small to medium-sized, filament medium length, lobe short to medium length. Penial ornament a medium-sized terminal gland.

Description: Shell (Figures 9I, 22K) narrow-conic, width/height, 59–69%; height, 1.6–2.0 mm; width, 1.0–1.3 mm; whorls, 4.25–5.0. Protoconch 1.25 whorls, diameter 0.34 mm, smooth except for small area of very weak wrinkling at apex. Teleoconch whorls low-medium convexity, narrowly shouldered, often having pronounced angulation at base; body whorl often broadly disjunct behind the aperture. Aperture ovate, usually disjunct. Inner lip thin, without columellar shelf. Outer lip thin, orthocline or weakly prosocline, without sinuation. Umbilicus rimate to shallowly perforate. Periostracum light tan.

Operculum ovate, amber; nucleus eccentric; dorsal surface weakly frilled. Attachment scar thick all around.

Radula 560 × 95 μm, with 62 rows of teeth. Central tooth 23 μm wide, with highly indented dorsal edge; lateral cusps, 5–7; central cusp narrow, daggerlike; basal cusps medium-sized. Basal tongue V-shaped, basal sockets deep. Lateral tooth formula 3(4)-1-4(5); neck weakly flexed; outer wing 225% of cutting edge length. Inner marginal teeth with 24–28 cusps; cutting edge occupying 33% of length of tooth. Outer marginal teeth with 25–30 cusps; cutting edge occupying 25% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented or having very light grey pigment proximally. Snout medium grey. Foot light

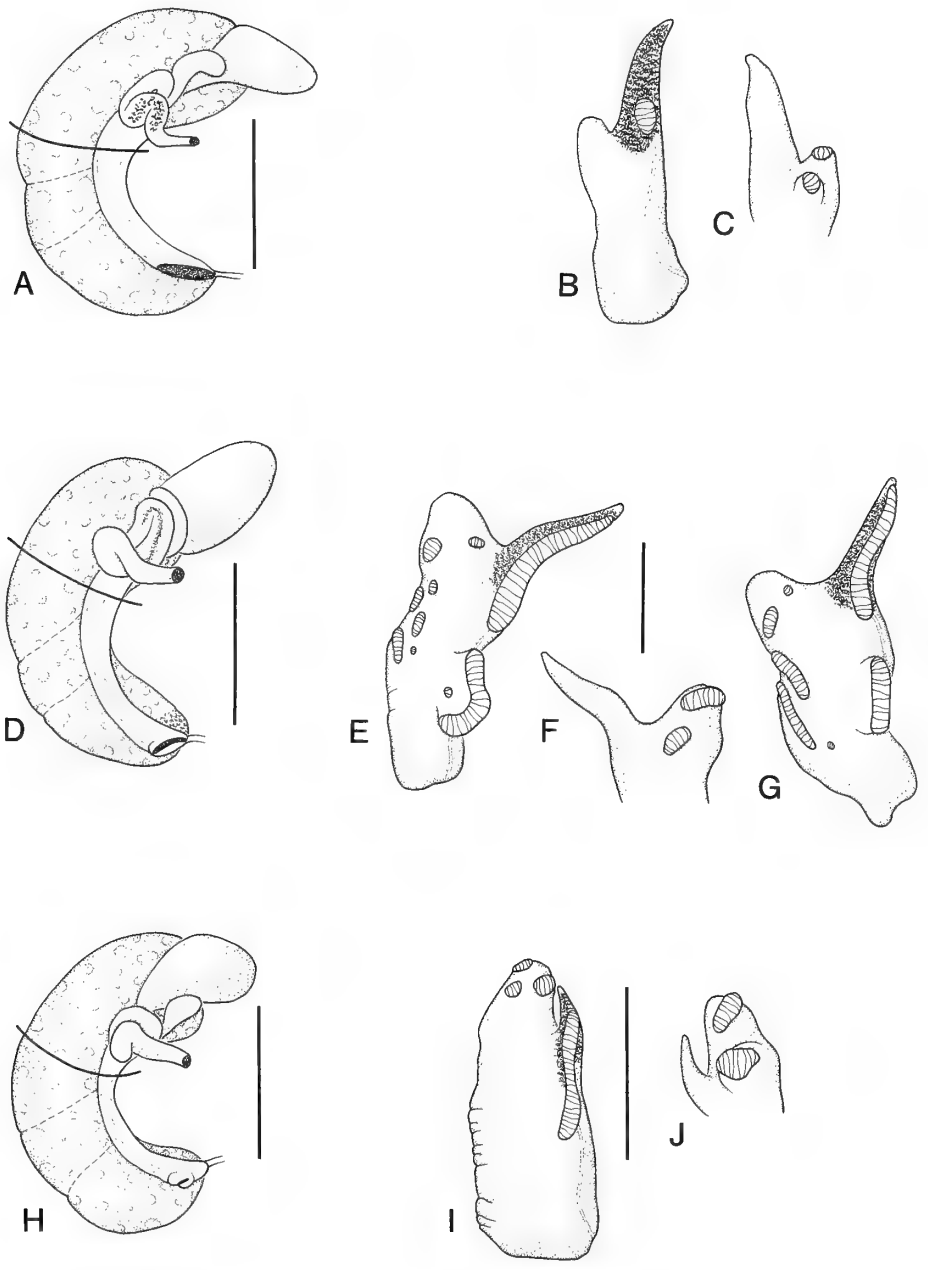


Figure 47

Genitalia of *Pyrgulopsis* species (A, *P. **fusca,*** USNM 860728; B, *P. **fusca,*** USNM 883484; D–G, *P. **chamberlini,*** USNM 860729; H–J, *P. **inopinata,*** USNM 860730). Bars = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis. Two examples of the dorsal penis (E, G) are shown for *P. **chamberlini.***

to medium grey. Opercular lobe dark along inner edge, sometimes along outer edge as well. Neck unpigmented except for scattered grey granules. Pallial roof, visceral coil near uniform black (pigment slightly lighter on genital ducts). Penial filament darkly pigmented internally for most of length.

Ctenidial filaments, 15, weakly pleated; ctenidium connected to pericardium by short efferent vein. Osphradium small, narrow, positioned slightly posterior to middle of ctenidium. Renal gland longitudinal; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.75 whorl, filling less than 50% of digestive

gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 43A. Albumen gland having medium (up to 33%) pallial component. Capsule gland shorter, narrower than albumen gland, ovate in section; rectal furrow medium depth. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit, mounted on weak papilla, having short anterior extention. Coiled oviduct a posterior-oblique loop sometimes preceded by weak to well-developed posterior twist. Bursa copulatrix medium length and width, ovate, longitudinal, slightly less than 33% of length posterior to gland. Bursal duct originating from anterior edge at mid-line, often poorly distinguished from bursa; short (up to 50% of bursa length), medium width. Seminal receptacle small, sometimes minute, pouchlike or sub-globular, overlapping anteriormost section of bursa.

Testis 1.5 whorls, filling more than 50% of digestive gland behind stomach, overlapping posterior and part of anterior stomach chambers. Prostate gland small, subglobular, pallial portion short, narrowly ovate in section. Proximal pallial vas deferens straight or having weak undulation. Penis (Figure 43B, C) small to medium-sized; base rectangular, weakly folded; filament 66% length of base, medium width, tapering to point, longitudinal or slightly oblique; lobe slightly shorter to as long as filament, clublike, longitudinal or slightly oblique. Terminal gland medium-sized, ovate or circular, rarely bifurcate, variably oriented, ventral. Penial duct straight, near outer edge.

Type locality: Springs, 0.5 km east of White Rock Cabin Springs, Hamlin Valley, Beaver County, Utah, T. 30 S, R. 20 W, SE ¼ section 2 (Figure 55). Holotype, USNM 883215 (Figure 22K), collected by R. Hershler and P. Hovingh, 9 May 1993; paratypes, USNM 860695. The type locality is a small, high elevation rheocrene slightly impacted by cattle (Figure 5D).

Remarks: This species is contrasted with *P. **montana*** above.

Material examined: UTAH. *Beaver County:* Springs, 0.5 km east of White Rock Cabin Springs (Figure 5D), USNM 860695, USNM 883215.

*Pyrgulopsis **peculiaris*** Hershler, sp. nov.

Bifid duct pyrg

(Figures 9J, 23A–G, 43D–I)

Etymology: From *peculiaris* (Latin), singular; referring to the unique configuration of the female bursal duct in this species.

Diagnosis: Medium-sized, with ovate- to narrow-conic shell. Penis large; filament and lobe medium length. Penial ornament a medium-large, fragmented terminal gland; small penial gland, large Dg1, large Dg2, large Dg3, additional four to seven dorsal glands, and two large ventral glands.

Description: Shell (Figures 9J, 23A–G) ovate to narrow conic, width/height, 62–89%; height, 1.7–3.0 mm; width, 1.3–2.1 mm; whorls, 3.5–5.0. Protoconch 1.25–1.5 whorls, diameter 0.34 mm, initial 0.5–1.0 whorl finely wrinkled, later portion smooth. Teleoconch whorls highly convex, shoulders weak to well developed; body whorl often slightly disjunct behind the aperture and having sub-sutural ramp bordered below by pronounced angulation. Aperture ovate, usually disjunct. Inner lip slightly thickened; columellar shelf very narrow to broad. Outer lip thin or slightly thickened, slightly prosocline, without sinuation. Umbilicus narrowly perforate. Periostracum light tan.

Operculum ovate, reddish; nucleus eccentric; dorsal surface weakly frilled; outer margin sometimes having weak rim. Attachment scar thick, sometimes broadly so, all around.

Radula 720 × 100 μm, with 57 rows of teeth. Central tooth 32 μm wide, with slightly indented dorsal edge; lateral cusps, 4; central cusp medium width, daggerlike; basal cusps medium-sized. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 2-1-3; neck weakly flexed; outer wing 130% of cutting edge length. Inner marginal teeth with 18–20 cusps; cutting edge occupying 36% of length of tooth. Outer marginal teeth with 27–31 cusps; cutting edge occupying 27% of length of tooth. Stomach larger than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles, snout, foot light to medium brown. Opercular lobe dark along inner edge, often all around. Neck unpigmented except for scattered dark granules to light brown. Pallial roof, visceral coil uniform dark brown to black. Penial filament darkly pigmented along most of length; adjacent portion of base similarly pigmented.

Ctenidial filaments, 16, without pleats; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, positioned slightly posterior to middle of ctenidium. Renal gland slightly oblique; kidney opening grey-white, slightly raised. Rectum broadly overlapping genital ducts.

Ovary 0.5–0.75 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 43D. Albumen gland having very short pallial component. Capsule gland longer, but narrower than albumen gland, broadly ovate in section; rectal furrow medium depth. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a posterior-oblique to almost circular loop; proximal arm sometimes kinked, usually darkly pigmented. Oviduct and bursal ducts joining a little behind pallial wall. Bursa

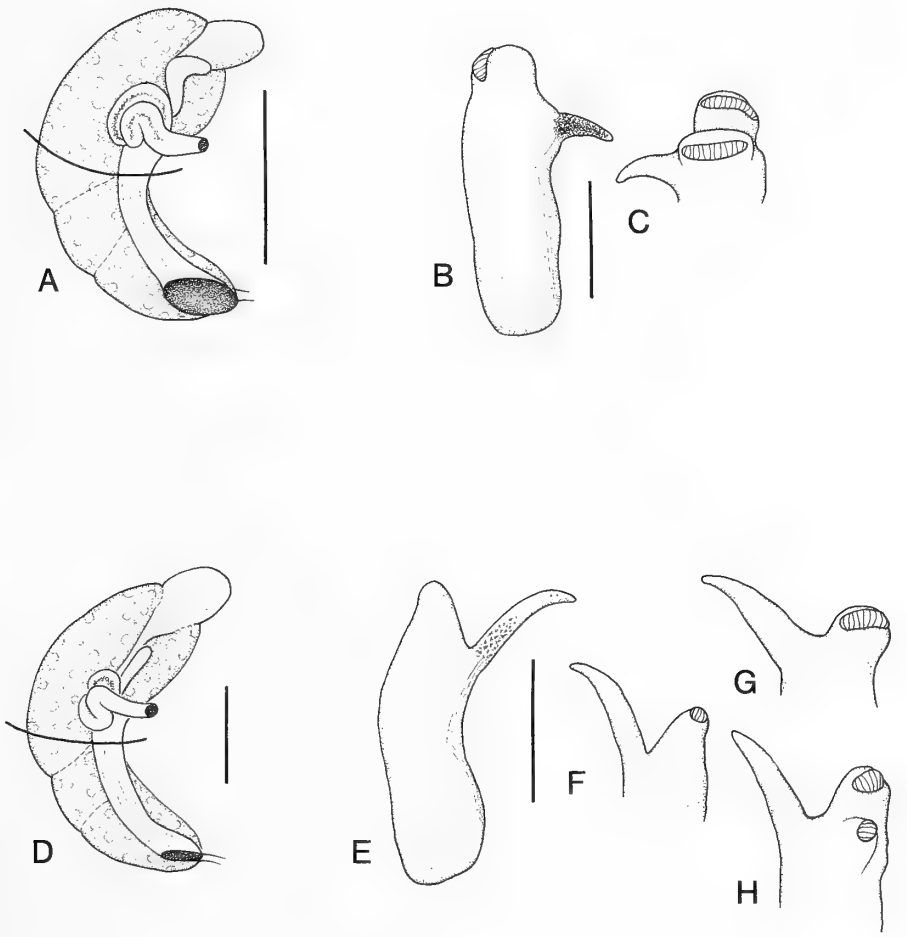


Figure 48

Genitalia of *Pyrgulopsis* species (A–C, *P.* ***nonaria,*** USNM 860731; D–F, *P.* ***transversa,*** USNM 860732; G, H, *P.* ***transversa,*** USNM 883422). A–C. Bars = 0.5 mm. D. Bar = 0.25 mm. E–H. Bar = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis. Three examples of the ventral penis (F–H) are illustrated for *P.* ***transversa.***

copulatrix medium length, but as wide as albumen gland, pyriform, longitudinal, with almost entire length posterior to gland. Bursal duct bifid (Figure 43E), consisting of duct originating from anterior edge at or near mid-line, medium length, narrow; and much narrower duct (of same length) originating from anterior edge near ventral margin; ducts share common opening to oviduct. Seminal receptacle a small, narrow pouch folded into an inverted U-shape, overlapping middle of bursa copulatrix.

Testis 1.0–1.25 whorls, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Prostate gland large, elongate bean-shaped, pallial portion short, ovate in section. Proximal pallial vas deferens having well-developed, reflexed loop; duct broad. Penis (Figure 43F–I) large; base rectangular, expanded distally, with pronounced swelling along inner edge, inner edge folded; filament medium length, narrow, tapering to point, usually oblique; lobe as long as filament, triangular, longitudinal. Terminal gland consisting of three short, ovate-circular units along edge of lobe (mostly ventral) unit along outer edge often fused with distal unit, occasionally all three units fused. Penial gland small, narrow, positioned near base of filament. Dg1 large (rarely reduced), positioned medially, usually transverse, sometimes fused with either Dg3 or outermost of additional longitudinal glands. Dg2 large, distal, borne on expanded edge of lobe. Dg3 large, extending to near base of filament (abutting or fusing with Dg1), sometimes curving across lobe, portion on lobe raised. Dorsal penis also bearing four to seven additional units (typically elongate, longitudinal, sometimes small, circular or dotlike) positioned between penial gland, Dg1 and Dg2; innermost units often fused distally. Ventral glands, two, large, distal gland narrow (sometimes accompanied distally by

raised, dotlike unit), borne on large swelling, traversing most of width of penis near base of filament; proximal gland shorter, broader, borne on prominent swelling, transverse, positioned near base of penis. Penial duct straight, near outer edge.

Type locality: Spring, Maple Grove, Round Valley, Millard County, Utah, T. 21 S, R. 2 1/2 W, NW ¼ section 1. Holotype, USNM 883933 (Figure 23A), collected by R. Hershler and P. Hovingh, 11 May 1995; paratypes, USNM 860703. The type locality is a small, montane rheocrene slightly disturbed by recreational activities.

Remarks: The penis of this snail somewhat resembles those of the group of species having a full complement of glands, but differs in that the penial gland is very small. Additionally, the terminal gland is weaker than in many members of this group, and a pronounced distal swelling is present along the inner edge of the penis base, a feature absent in the above species but similar to that of *P. **limaria,*** from northwest Lahontan Basin. This species is also unique among *Pyrgulopsis* in having a bifid bursal duct, a condition apparently paralleling that seen in *Cincinnatia integra* (see Hershler & Thompson, 1996). The distribution of this species is shown in Figure 55.

Material examined: NEVADA. *White Pine County:* Springs, Big Springs Creek, Snake Valley, T. 10 N, R. 70 E, SW ¼ section 22, USNM 874683.—Turnley Spring, Spring Valley, T. 16 N, R. 68 E, SW ¼ section 16, USNM 874319, USNM 874666. UTAH. *Millard County:* Spring, Maple Grove, USNM 860703, USNM 883602, USNM 883933.—Church Spring, Pahvant Valley, T Spring, T. 19 S, R. 4 W, NE ¼ section 14, USNM 892053.—South Fork Chalk Creek, Pahvant Valley, T. 22 S, R. 3 W, NW ¼ section 6, USNM 883603.—Big Spring, Oak Creek, Sevier River drainage, T. 17 S, R. 4 W, NW ¼ section 12, USNM 883622.—Spring, above Swasey Spring, Whirlwind Valley, T. 16 S, R. 13 W, SW ¼ section 23, USNM 883222.—Antelope Spring, House Range, Sevier Desert drainage, T. 16 S, R. 13 W, NE ¼ section 34, USNM 883227.

*Pyrgulopsis **anguina*** Hershler, sp. nov.

Longitudinal gland pyrg

(Figures 9K, 23H–J, 44A–E)

Etymology: From *anguinus* (Latin), of snakes; referring to endemism of this species in Snake Valley, Nevada-Utah.

Diagnosis: Medium-sized, with sub-globose to ovate-conic shell. Penis large; filament and lobe short. Penial ornament a medium-sized terminal gland, large penial gland, medium-large Dg1, large Dg2, medium-large Dg3, additional dorsal gland, and large ventral gland.

Description: Shell (Figures 9K, 23H–J) sub-globose to ovate-conic, apex often eroded; width/height, 70–95%; height, 2.0–3.5 mm; width, 1.7–2.4 mm; whorls, 3.0–5.0. Protoconch 1.25 whorls, diameter 0.30 mm, weakly wrinkled at apex, otherwise smooth. Teleoconch whorls medium to highly convex, shoulders narrow or absent, sculpture including faint spiral striae; body whorl often slightly disjunct behind the aperture. Aperture pyriform, adnate or disjunct. Inner lip slightly thickened in larger specimens, often forming narrow columellar shelf. Outer lip thin, slightly prosocline, without sinuation. Umbilicus shallowly perforate. Periostracum tan-green.

Operculum ovate, amber, nuclear region slightly reddish; nucleus eccentric; dorsal surface frilled. Attachment scar often thick all around.

Radula 820 × 120 μm, with 62 rows of teeth. Central tooth 26 μm wide, with medium-highly indented dorsal edge; lateral cusps, 5–7; central cusp medium width, rounded; basal cusps large. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 2(3)-1-4(5); neck medium flexed; outer wing 195% of cutting edge length. Inner marginal teeth with 27–34 cusps (basal enlarged, separated); cutting edge occupying 43% of length of tooth. Outer marginal teeth with 32–40 cusps; cutting edge occupying 26% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented to medium brown. Snout, foot light to medium brown. Opercular lobe dark along inner edge, sometimes also along sides. Neck unpigmented except for scattered granules to medium brown. Pallial roof, visceral coil uniformly dark brown or black. Penial filament darkly pigmented along almost entire length; black granules sometimes scattered on remainder of penis.

Ctenidial filaments, 18, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, positioned posterior to middle of ctenidium. Renal gland slightly oblique; kidney opening thick, white. Rectum broadly overlapping genital ducts.

Ovary 0.75 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 44A. Albumen gland having large (ca. 40%) pallial component. Capsule gland shorter, narrower than albumen gland, subglobular in section; rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit, sometimes mounted on weak papilla, having short anterior extension. Coiled oviduct of two overlapping posterior-oblique loops; posterior loop often overlapping bursa copulatrix. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix as long and wide as albumen gland, ovate-pyriform, longitudinal, with most or all of length posterior to gland. Bursal duct originating from anterior edge at or near mid-line and close to oviduct;

very short (20%), narrow. Seminal receptacle very small, pouchlike, overlapping anterior half of bursa.

Testis 1.25–1.5 whorls, filling almost all of digestive gland behind stomach, overlapping posterior and part of anterior stomach chambers. Prostate gland very large, elongate bean-shaped, pallial portion large (almost 50%), ovate in section. Proximal pallial vas deferens having well-developed, reflexed loop; duct broad. Penis (Figure 44B–E) large; base rectangular, sometimes slightly expanded distally, weakly folded; filament short, medium width, tapering to point, longitudinal or slightly oblique; lobe as long as filament, triangular, longitudinal. Terminal gland medium-sized, narrow, longitudinal, largely or entirely ventral. Penial gland filling most of length of filament and slightly overlapping base, slightly narrower than filament. Dg1 medium-large, narrow, slightly or prominently raised, sometimes slightly curved, longitudinal or slightly oblique, positioned near mid-length at or near outer edge. Dg2 large, sometimes bifurcate, slightly raised or crestlike, positioned along inner edge. Dg3 medium-large, narrow, positioned near outer edge of lobe. Dorsal penis also bearing long gland (rarely bifurcate) near inner edge distally (extending distal to Dg2 and slightly overlapping lobe), often fused with Dg3 to form U-shaped loop. Small, circular glands sometimes found alongside Dg1 and Dg2, just proximal to edge of Dg3. Ventral gland large, usually narrow (rarely small, circular), borne on prominent swelling, usually straight and transverse, but sometimes curved; positioned near base of lobe. Penial duct straight, near outer edge.

Type locality: Big Springs, Snake Valley, White Pine County, Nevada, T. 10 N, R. 70 E, NE ¼ section 33. Holotype, USNM 874678 (Figure 23H), collected by R. Hershler and P. Hovingh, 23 June 1992; paratypes, USNM 860725. The type locality is a shallow, 4 m wide rheocrene moderately disturbed by livestock.

Remarks: Among the group of species having a full complement of penial ornament, *P. **anguina*** most closely resembles *P. **chamberlini*** (described below), from Sevier River drainage, but differs in its broader shell, larger penial lobe, longitudinal orientation of terminal gland, and stronger Dg3 and ventral gland. The distribution of *P. **anguina*** is shown in Figure 55.

Material examined: NEVADA. *White Pine County:* Big Springs, Snake Valley, USNM 860725, USNM 874678. UTAH. *Millard County:* Clay Spring, Snake Valley, T. 22 S, R. 19 W, NW ¼ section 33, USNM 883205.

*Pyrgulopsis **saxatilis*** Hershler, sp. nov.

Sub-globose Snake pyrg

(Figures 9L, 11H, 16A–C, 23K, L, 44F–H)

Etymology: From *saxatilis* (Latin), found among rocks; referring to the habitat of species.

Diagnosis: Small, with sub-globose shell. Penis large, filament and lobe short. Penial ornament a small terminal gland, small Dg1, and large ventral gland.

Description: Shell (Figures 9L, 23K, L) sub-globose, apex usually eroded in adult apecimens; width/height, 90–106%; height, 1.0–1.4 mm; width, 1.0–1.4 mm; whorls, 3.5–4.0. Protoconch (Figure 11H) 1.25 whorls, diameter 0.28 mm; initial 0.75 whorl finely wrinkled. Teleoconch whorls medium convexity; shoulders well developed, final 0.25 whorl sometimes having pronounced sub-sutural angulation. Aperture ovate-pyriform, adnate. Inner lip slightly thickened, columellar shelf medium width. Outer lip thin, prosocline, weakly sinuate. Umbilicus narrowly rimate to shallowly perforate. Periostracum eroded or absent.

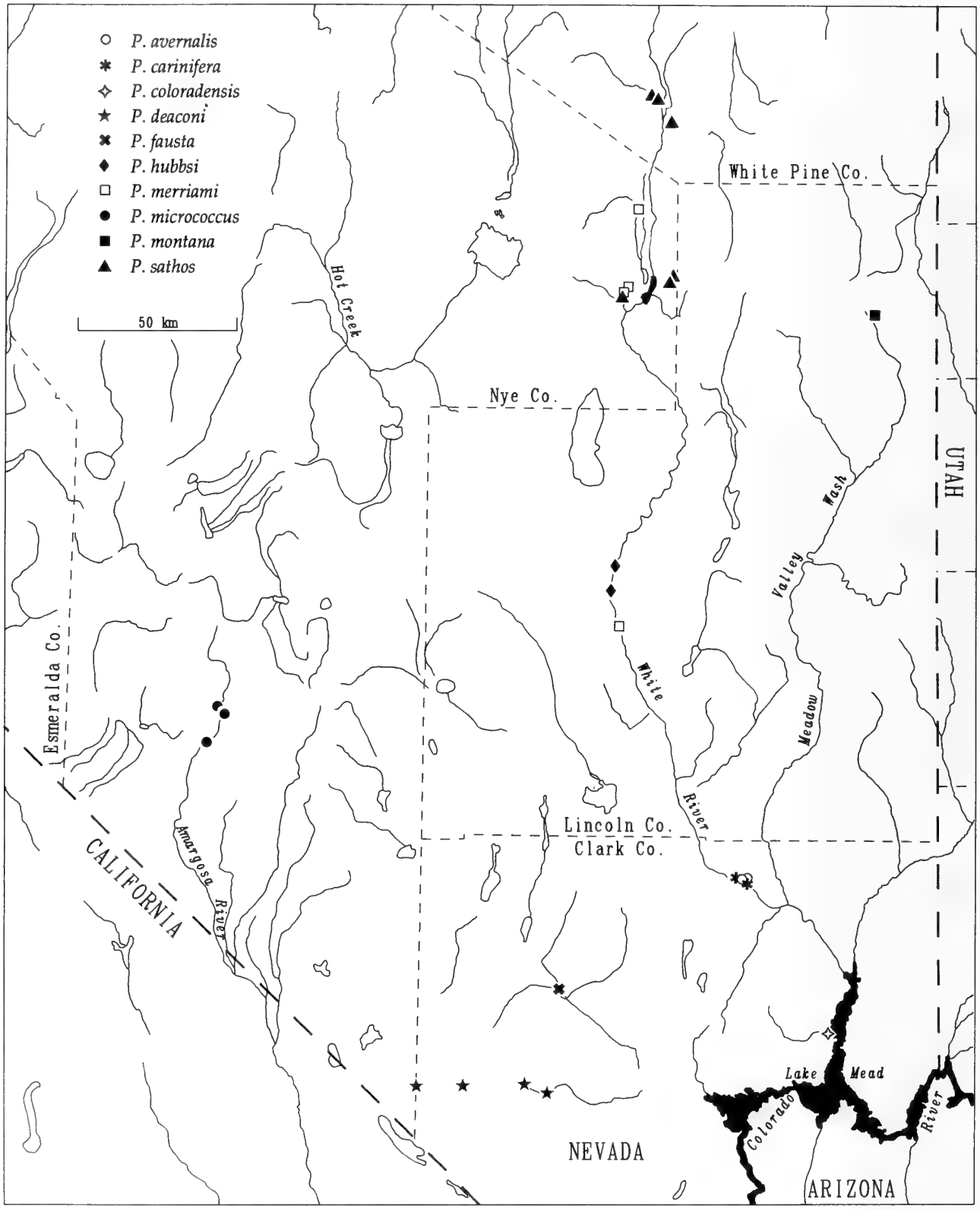
Operculum ovate, amber, slightly darker in nuclear region; dorsal surface smooth or weakly frilled; outer margin sometimes having very faint rim. Attachment scar thick along inner edge and between inner edge and nucleus.

Radula (Figure 16A–C) 480 × 65 μm, with 60 rows of teeth. Central tooth 15 μm wide, with highly indented dorsal edge; lateral cusps, 5–7; central cusp long, daggerlike; basal cusps medium-sized. Basal tongue broad V-shaped, basal sockets medium depth. Lateral tooth formula 3-1-4(5); neck weakly flexed; outer wing 200% of cutting edge length. Inner marginal teeth with 22–25 cusps; cutting edge occupying 36% of length of tooth. Outer marginal teeth with 24–27 cusps; cutting edge occupying 29% of length of tooth. Stomach longer than style sac; stomach chambers poorly distinguished externally, but anterior chamber slightly larger; stomach caecum very small.

Cephalic tentacles, foot light to medium brown. Snout medium to dark brown. Opercular lobe unpigmented or diffuse light brown. Neck light to medium grey-brown. Pallial roof, visceral coil uniformly dark brown or black. Penial filament darkly pigmented along most of length; base also containing scattered black granules.

Ctenidial filaments, 12, without pleats; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow ovate, positioned slightly posterior to middle of ctenidium. Renal gland oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.5–0.75 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 44F. Albumen gland having short pallial component. Capsule gland shorter, narrower than albumen gland, ovate in section; rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold weakly developed. Genital aperture a terminal slit mounted on weak papilla, anterior extension short. Coiled oviduct a small circular loop, usually preceded by well-developed posterior twist. Oviduct and bursal duct joining a little behind


P. avernalis
P. carinifera
P. coloradensis
P. deaconi
P. fausta
P. hubbsi
P. merriami
P. micrococcus
P. montana
P. sathos
50 km
Hot Creek
White Pine Co.
Nye Co.
Esmeralda Co.
CALIFORNIA
Amargosa River
Lincoln Co.
Clark Co.
White River
Meadow Valley Wash
UTAH
NEVADA
ARIZONA
Lake Mead
Colorado River

pallial wall. Bursa copulatrix short, narrow, globular-pyriform, longitudinal, with most of length posterior to gland. Bursal duct originating from anterior edge at midline, long, narrow to medium width. Seminal receptacle small to medium-sized, pouchlike, overlapping proximal to medial portion of bursal duct, often overlapped by albumen gland.

Testis 1.0 whorl, filling 50% of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland bean-shaped, pallial portion short, narrowly ovate in section. Proximal pallial vas deferens with well-developed loop. Penis (Figure 44G, H) large; base elongate-rectangular, smooth or weakly folded along inner edge; filament short, narrow, tapering to point, longitudinal or slightly oblique; lobe as long as filament, clublike, but narrowing distally, longitudinal. Terminal gland small, circular to ovate (usually transverse), ventral. Dg1 small, ovate, longitudinal or slightly oblique, positioned just proximal to base of filament. Ventral gland large, narrow, slightly raised, angling across penis to base of lobe at inner edge. Dorsal and ventral penis also frequently having one to six minute, variably positioned, glandular dots. Penial duct slightly undulating near outer edge distally.

Type locality: Warm Springs, Snake Valley, Millard County, Utah, T. 16 S, R. 19 W, SW ¼ section 31 (Figure 55). Holotype, USNM 883237 (Figure 23K), collected by R. Hershler and P. Hovingh, 10 May 1993; paratypes, USNM 860726. The type locality is a series of large, thermal (26.9°C) rheocrenes issuing from the side of a hill.

Remarks: This thermal endemic is contrasted above with *P. **lata,*** from White River Valley. *Pyrgulopsis **saxatilis*** also resembles widespread *P. kolobensis,* but differs in its minute, globose shell, narrower central cusps on the central radular teeth, more elongate outer wing on the lateral radular teeth, smaller penial lobe and filament, and weakly developed terminal gland.

Material examined: UTAH. *Millard County:* Warm Springs, USNM 860726, USNM 883237.

*Pyrgulopsis **variegata*** Hershler, sp. nov.

Northwest Bonneville pyrg

(Figures 10A, 24A–D, 45A–F)

Etymology: From *variegatus* (Latin), of different sorts; referring to the substantial variation in penial glands among populations assigned to this species.

Diagnosis: Medium-sized, with ovate- to narrow-conic shell. Penis small to large, filament and lobe medium length. Penial ornament a small terminal gland, very small penial gland (often absent), and small ventral gland (often absent).

Description: Shell (Figures 10A, 24A–D) ovate- to narrow-conic, width/height, 63–75%; height, 2.2–3.0 mm; width, 1.5–2.4 mm; whorls, 4.25–5.0. Protoconch 1.4–1.5 whorls, diameter 0.33 mm; smooth except for weak spiral striae along outer edge of whorl. Teleoconch whorls medium to highly convex, shoulders weak or absent; body whorl often slightly disjunct behind the aperture. Aperture ovate, usually disjunct. Inner lip slightly thickened in largest specimens, without columellar shelf. Outer lip thin, prosocline, without sinuation. Umbilicus rimate or shallowly perforate. Periostracum light or reddish-brown.

Operculum ovate, amber, nuclear region reddish; nucleus eccentric; outer margin having weak rim. Attachment scar thick all around.

Radula 665 × 105 μm, with 62 rows of teeth. Central tooth 26 μm wide, with medium indented dorsal edge; lateral cusps, 5–7, central cusp medium width, rounded; basal cusps medium-sized. Basal process V-shaped, basal sockets medium depth. Lateral tooth formula 3(4)-1-3(4, 5); neck weakly flexed; outer wing 185% of cutting edge length. Inner marginal teeth with 25–31 cusps (basal cusp enlarged); cutting edge occupying 35% of length of tooth. Outer marginal teeth with 31–36 cusps; cutting edge occupying 25% of length of tooth. Stomach longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small or very small.

Cephalic tentacles unpigmented or having proximal light grey patch. Snout, foot light to medium grey. Opercular lobe black along inner edge. Neck unpigmented except for scattered black granules to medium grey. Pallial roof, visceral coil medium grey to black, pigment non-uniform. Penial filament darkly pigmented; pigment granules scattered on base.

Ctenidium medium width; filaments, 17, without pleats; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, centered well posterior to middle of ctenidium. Renal gland oblique; kidney opening grey-white. Rectum straight, broadly overlapping genital ducts.

Ovary 0.75–1.0 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 45A.

←

Figure 49

Map showing distributions of *Pyrgulopsis* species of southern Nevada. Previously known records for *P. micrococcus, P. avernalis, P. carinifera,* and *P. merriami* are not shown. In cases where congeners are sympatric, symbols are slightly offset.

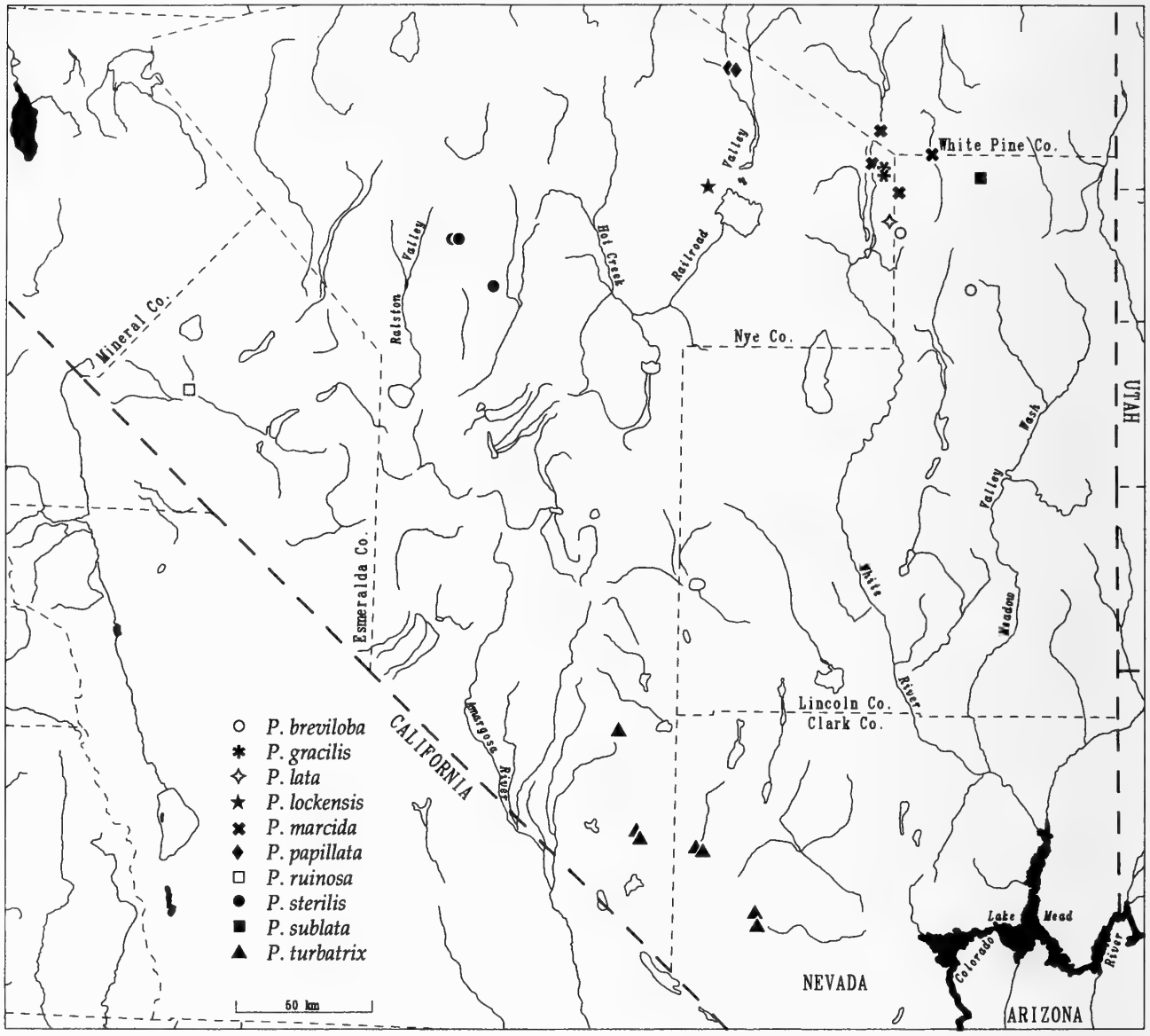


Figure 50

Map showing distributions of *Pyrgulopsis* species of the Colorado River drainage basin and isolated basins of Nevada. In cases where congeners are sympatric, symbols are slightly offset.

Albumen gland having short pallial component. Capsule gland shorter, narrower than albumen gland, circular in section; rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal pore often mounted on weak papilla; anterior extension short. Coiled oviduct a posterior-oblique loop often preceded by weak posterior-oblique twist. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix short, medium width, pyriform, often having silvery sheen, longitudinal, with 50% or more of length usually posterior to gland, dorsal edge sometimes slightly overlapped by gland. Bursal duct originating from anterior edge at mid-line, slightly shorter to slightly longer than bursa, medium width. Seminal receptacle small, pouchlike, overlapping or slightly ventral to proximal portion of bursal duct.

Testis 1.5 whorls, filling more than 50% of digestive gland behind stomach, overlapping posterior and portion of anterior stomach chamber. Prostate gland small, subglobular, entirely visceral or with very short pallial portion, narrowly ovate in section. Proximal pallial vas deferens looped. Penis (Figure 45B–F) small to large; base

rectangular, sometimes elongate, folds along inner edge weak to well developed; filament 50% to almost as long as base, medium width, tapering to point, longitudinal or slightly oblique; lobe shorter than filament, slightly narrower than base, knoblike, longitudinal. Terminal gland small, rarely dotlike, narrow, circular-ovate, usually transverse (rarely longitudinal), entirely ventral or partly overlapping dorsal surface. Penial gland very small (often absent), narrow, positioned near base of filament. Ventral gland small (often absent), ovate-narrow, often slightly raised, longitudinal, distal. Penial duct straight, near outer edge.

Type locality: Spring, ca. 2.5 km south of South Patterson Spring, Pilot Valley, Box Elder County, Utah, T. 4 N, R. 19 W, SW ¼ section 1. Holotype, USNM 883627 (Figure 24A), collected by R. Hershler and P. Hovingh, 9 July 1993; paratypes, USNM 860723. The type locality is a small, minimally disturbed basin floor rheocrene.

Remarks: This species differs from similar *P. kolobensis* in having a smaller penial lobe and reduced (sometimes absent) glands on the penis. Populations of this species from the south and west have relatively well developed penial and terminal glands, and a weak or absent ventral glands; while those to the north and east (e.g., Grouse Creek, Park Valleys) have weak terminal gland, often lack a penial gland, and have stronger ventral glands. However, intergradation between these two conditions is evident in some populations, in which the penis has a well-developed penial gland, but weak terminal and ventral glands. The distribution of this species is shown in Figure 55.

Material examined: NEVADA. *Elko County:* Parson Springs, Pilot Creek Valley, T. 38 N, R. 70 E, NE ¼ section 28, USNM 874713.—McCuistion Springs, Pilot Creek Valley, T. 37 N, R. 70 E, NE ¼ section 30, USNM 874723, USNM 883888.—Spring, lower Jay Creek, Goose Creek drainage, T 47N, R 69E, SW ¼ section 23, USNM 874721. UTAH. *Box Elder County:* Spring, ca. 2.5 km south of South Patterson Spring, USNM 860723, USNM 883627.—Spring, Halls Meadow, T. 3 N, R. 19 W, section 22, USNM 873431.—Spring, Cotton Creek, Grouse Creek Valley, T. 13 N, R. 17 W, SE ¼ section 29, USNM 883636.—Spring, Cotton Creek, Grouse Creek Valley, T. 13 N, R. 17 W, section 32, UCM 34042.—Spring brook, tributary to Etna Reservoir, Grouse Creek Valley (Figure 5E), T. 11 N, R. 18 W, NW ¼ section 6, USNM 883614.—North Bedke Spring, Grouse Creek Valley, T. 11 N, R. 17 W, NW ¼ section 32, USNM 883624.—South Bedke Spring, Grouse Creek Valley, T. 11 N, R. 17 W, SE ¼ section 31, USNM 883583—Spring, Left Hand Fork, Dove Creek, Park Valley (Figure 3C), T. 13 N, R. 16 W, NE ¼ section 26, USNM 883599. *Tooele County:* Spring, ca. 4.8 km south of Donner Spring, Pilot Valley, T. 3 N, R. 19 W, center section 14, USNM 883608.

Pyrgulopsis ***hovinghi*** Hershler, sp. nov.

Upper Thousand Spring pyrg

(Figures 10B, 111, 16D–F, 24E, 45G–I)

Etymology: Named after Peter Hovingh, in recognition of his extensive support and encouragement throughout this study.

Diagnosis: Medium-sized, with sub-globose to ovate-conic shell. Penis small to medium-sized; filament and lobe medium length. Penial ornament a large penial gland.

Description: Shell (Figures 10B, 24E) sub-globose to ovate-conic, apex and early teleoconch often eroded; width/height, 67–80%; height, 2.2–2.8 mm; width, 1.7–2.0 mm; whorls, 4.0–4.75. Protoconch (Figure 111) 1.2 whorls, 0.32 mm, initial 0.75 whorl finely (sometimes strongly) wrinkled, later portion near smooth. Teleoconch whorls highly convex, shoulders well developed, sculpture including well-developed spiral striae; body whorl often slightly disjunct behind the aperture. Aperture ovate, narrowly adnate or slightly disjunct. Inner lip slightly thickened, sometimes forming narrow columellar shelf. Outer lip thin, orthocline to slightly prosocline, sinuate. Umbilicus rimate or shallowly perforate. Periostracum dark tan or brown.

Operculum ovate, dark amber; nucleus eccentric; dorsal surface frilled; outer margin sometimes having weak rim. Attachment scar thick all around.

Radula (Figure 16D–F) 675 × 110 μm, with 50 rows of teeth. Central tooth 26 μm wide, with highly indented dorsal edge; lateral cusps, 4–6; central cusp long, narrow, daggerlike; basal cusps medium-large. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 2(3)-1-4; neck weak; outer wing 180% of cutting edge length. Inner marginal teeth with 27–32 cusps (basal cusp enlarged); cutting edge occupying 34% of length of tooth. Outer marginal teeth with 30–37 cusps; cutting edge occupying 27% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles light to medium brown. Snout medium to dark brown or black. Foot medium to dark brown. Opercular lobe black along inner edge, elsewhere unpigmented to medium grey-black. Neck unpigmented except for scattered black granules to almost uniform black. Pallial roof, visceral coil black, pigment slightly lighter on genital ducts. Penial filament darkly pigmented; pigment granules sometimes also scattered on base.

Ctenidial filaments, 19, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, positioned well posterior to middle of ctenidium. Renal

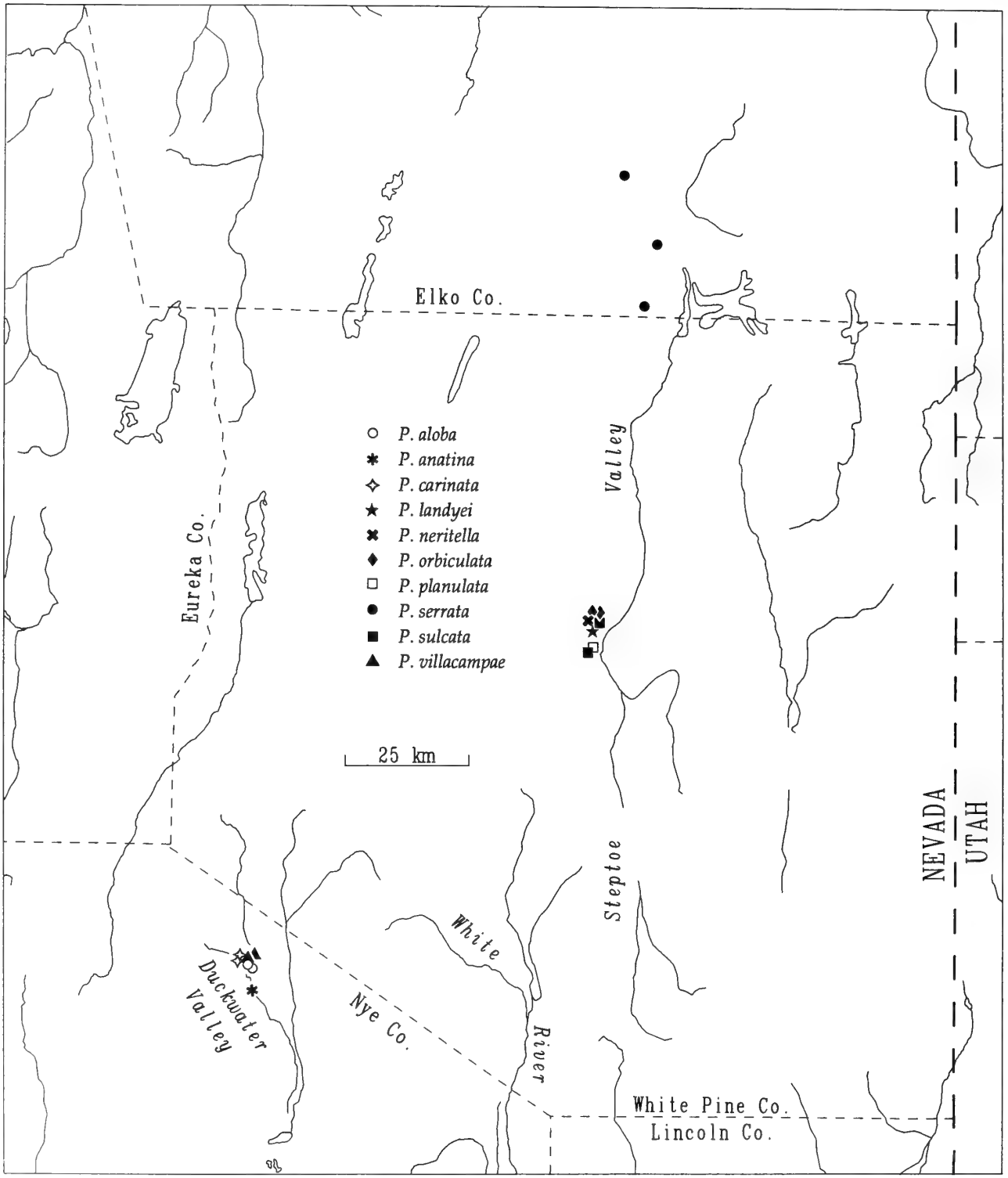


Figure 51

Map showing distributions of locally endemic *Pyrgulopsis* species of Duckwater and Steptoe Valleys, Nevada. In cases where congeners are sympatric, symbols are slightly offset.

gland slightly oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.5–0.75 whorl, filling more than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 45G. Albumen gland having short pallial component. Capsule gland sub-equal to albumen gland in length and width, sub-globular in section, rectal furrow well developed. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a sub-terminal pore having short anterior extension. Coiled oviduct a small, posterior-oblique loop preceded and overlapped by weak twist (sometimes forming a similar posterior-oblique loop). Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix short, almost as wide as albumen gland, sub-globular to ovate, longitudinal, with 33–50% of length posterior to gland. Bursal duct originating from anterior edge at mid-line, 66% of bursa length, medium width. Seminal receptacle small, pouchlike, lateral to proximal portion of bursal duct, positioned near ventral edge of albumen gland.

Testis 1.0–1.25 whorls, filling almost all of digestive gland behind stomach, overlapping posterior and part of anterior stomach chamber. Prostate gland bean-shaped, pallial portion short, ovate in section. Proximal pallial vas deferens having well-developed, often reflexed loop, duct broad. Penis (Figure 45H, I) small to medium-sized; base rectangular, often expanded distally, weakly folded; filament medium length, narrow, often curved, tapering to point, longitudinal; lobe slightly shorter to as long as filament, clublike to hemispherical, longitudinal or slightly oblique. Penial gland large, narrow, slightly raised, positioned along outer edge of proximal filament and distal base. Penial duct straight, near outer edge.

Type locality: Prather Springs, Thousand Springs Valley, Elko County, Nevada, T. 40 N, R. 64 E, SE ¼ section 21 (Figure 56). Holotype, USNM 874075 (Figure 24E), collected by P. Hovingh, 18 September 1990; paratypes, USNM 860720. The type locality is a small rheocrene moderately impacted by cattle.

Remarks: While *P.* ***hovinghi*** is similar to the other two species endemic to the Thousand Springs drainage (described below) in some respects, particularly the configuration of the distal female genitalia, these snails are heterogenous in penial and other features and probably do not compose a clade. *Pyrgulopsis* ***hovinghi*** differs from the above in having narrower central cusps on the central radular teeth, and is distinguished from these as well as all other congeners by its unique penial ornament, consisting solely of an elongate Dg1 positioned just behind the penial filament.

Material examined: NEVADA. *Elko County:* Prather Springs, USNM 860720, USNM 874075, USNM 874715.

Pyrgulopsis ***millenaria*** Hershler, sp. nov.

Twentyone Mile pyrg

(Figures 10C, 24F, 46A, B)

Etymology: From *millenarius* (Latin), of a thousand; referring to the endemism of this snail in the Thousand Springs Creek drainage, Nevada.

Diagnosis: Medium-sized, with ovate-conic shell. Penis small; filament medium length, lobe absent. Penial ornament absent.

Description: Shell (Figures 10C, 24F) ovate-conic, width/height, 67–78%; height, 2.4–3.1 mm; width, 1.8–2.3 mm; whorls, 4.0–4.75. Protoconch 1.25 whorls, diameter 0.27 mm, smooth except for very small, finely wrinkled area at apex. Teleoconch whorls medium convexity, weakly shouldered; sculpture including faint spiral striae. Aperture ovate, broadly adnate to very slightly disjunct. Inner lip thin, columellar shelf absent or very narrow. Outer lip thin, orthocline, without sinuation. Umbilicus rimate. Periostracum tan.

Operculum ovate, amber; nucleus eccentric; dorsal surface frilled. Attachment scar thick all around.

Radula 780 × 135 μm, with 47 rows of teeth. Central tooth 36 μm wide, with weakly indented dorsal edge; lateral cusps, 4–5; central cusp medium width, considerably longer than laterals, daggerlike or rounded; basal cusps medium-sized. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 2-1-2(3, 4); neck weakly flexed; outer wing 170% of cutting edge length. Inner marginal teeth with 19–22 cusps; cutting edge occupying 33% of length of tooth. Outer marginal teeth with 26–31 cusps; cutting edge occupying 25% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented or having light brown patch proximally. Snout light to dark brown. Foot unpigmented or light brown. Opercular lobe medium to dark brown along sides; small central zone unpigmented. Neck unpigmented or having scattered grey-brown granules. Pallial roof, visceral coil medium brown-black; pigment not uniform. Penial filament darkly pigmented internally.

Ctenidial filaments, 19; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, positioned well posterior to middle of ctenidium. Renal gland longitudinal or slightly oblique; kidney opening grey-white. Rectum broadly overlapping pallial oviduct, slightly overlapping prostate gland.

Ovary 0.5 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 46A. Albumen gland having short or no pallial component. Capsule gland as long and slightly narrower than albumen gland, ovate in section; rectal furrow very weak. Ventral

channel broadly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a posterior-oblique loop sometimes preceded by posterior-oblique twist, coil sometimes kinked or twisted at mid-line. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, positioned along ventral margin of gland, sub-globose to ovate, usually having silvery sheen, longitudinal, with 33% or less of length posterior to gland. Bursal duct originating from anterior edge at mid-line, 66–100% length of bursa, medium width. Seminal receptacle small, narrow pouchlike, overlapping or ventral to anterior half of bursa, sometimes partly overlapped by albumen gland.

Testis 1.5–1.75 whorls, filling more than 50% of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland small, sub-globose, pallial portion very short, narrowly ovate in section. Proximal pallial vas deferens looped. Penis (Figure 46B) small; base rectangular, strongly folded along inner edge; filament medium length, broad, muscular, tapering, longitudinal; lobe absent, distal edge of penis blunt; glands absent. Penial duct straight, near outer edge.

Type locality: Springs, below Twentyone Mile Dam, Thousand Springs Creek, Elko County, Nevada, T. 42 N, R. 67 E, SW ¼ section 14 (Figure 56). Holotype, USNM 874720 (Figure 24F), collected by R. Hershler and P. Hovingh, 30 August 1992; paratypes, USNM 860721. The type locality is a small rheocrene (Figure 5F).

Remarks: *Pyrgulopsis* ***millenaria*** differs from other species locally endemic in Thousand Springs drainage in having a much smoother protoconch and bursa copulatrix positioned near the ventral margin of the albumen gland. It is further distinguished from these and other species in the region in consistently lacking both a penial lobe and penial glands. This snail does not closely resemble other Great Basin species that have a simple penis.

Material examined: NEVADA. *Elko County:* Springs, below Twentyone Mile Dam (Figure 5F), USNM 860721, USNM 873329, USNM 874720.

Pyrgulopsis ***lentiglans*** Hershler, sp. nov.

Crittenden pyrg

(Figures 10D, 24G, H, 46C–E)

Etymology: From *lentis* (Latin), lentil-shaped; and *glans,* gland; referring to the dotlike terminal gland on the penis of this species.

Diagnosis: Small, with ovate-conic to pupiform shell. Penis large, filament medium length, lobe short or absent. Penial ornament a very small terminal gland (often absent).

Description: Shell (Figures 10D, 24G, H) ovate-conic to pupiform, width/height, 58–71%; height, 1.4–1.8 mm; width, 0.9–1.2 mm; whorls, 4.25–4.75. Protoconch 1.2 whorls, diameter 0.27 mm, initial 0.75 whorl finely wrinkled, otherwise smooth. Teleoconch whorls low to medium convexity, without shoulders, sculpture including faint spiral striae; body whorl often slightly disjunct behind the aperture. Aperture ovate, usually slightly disjunct. Inner lip slightly thickened, without columellar shelf. Outer lip thin, prosocline, sometimes weakly sinuate. Umbilicus rimate to shallowly perforate. Periostracum tan.

Operculum ovate, amber; nucleus eccentric; dorsal surface strongly frilled; outer margin sometimes having weak rim. Attachment scar strongly thickened between nucleus and inner edge, slightly thickened along inner edge.

Radula 440 × 70 μm, with 60 rows of teeth. Central tooth 15 μm wide, with highly indented dorsal edge; lateral cusps, 4–6; central cusp medium width, spoon-shaped; basal cusps medium-large, sometimes accompanied by weak thickenings to outside. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 3–1–4; neck weakly flexed; outer wing 225% of cutting edge length. Inner marginal teeth with 24–26 cusps; cutting edge occupying 33% of length of tooth. Outer marginal teeth with 26–32 cusps; cutting edge occupying 25% of length of tooth. Stomach as long as style sac; stomach chambers equal-sized; stomach caecum very small.

Cephalic tentacles unpigmented to medium brown. Snout light to dark brown. Foot light brown. Opercular lobe nearly unpigmented or having light, diffuse, grey pigment all around. Neck unpigmented except for scattered granules to light brown. Pallial roof, visceral coil medium to dark brown, sometimes uniformly pigmented. Penial filament darkly pigmented for almost entire length; base having scattered black granules.

Ctenidial filaments, 15, pleated; ctenidium connected to pericardium by short efferent vein. Osphradium 33% of ctenidium length, narrow, positioned posterior to middle of ctenidium. Renal gland longitudinal or slightly oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.5–0.75 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 46C. Albumen gland having medium pallial component. Capsule gland shorter, narrower than albumen gland, ovate in section; rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal pore sometimes expanded or mounted on weak papilla; anterior extension absent. Coiled oviduct a posterior-oblique loop, often kinked at mid-length and/or preceded by small posterior twist. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, sub-globular to ovate, often having silvery sheen, longitudinal or slightly oblique (anterior end dorsal), with 50–80% of length posterior to gland. Bursal duct originating from

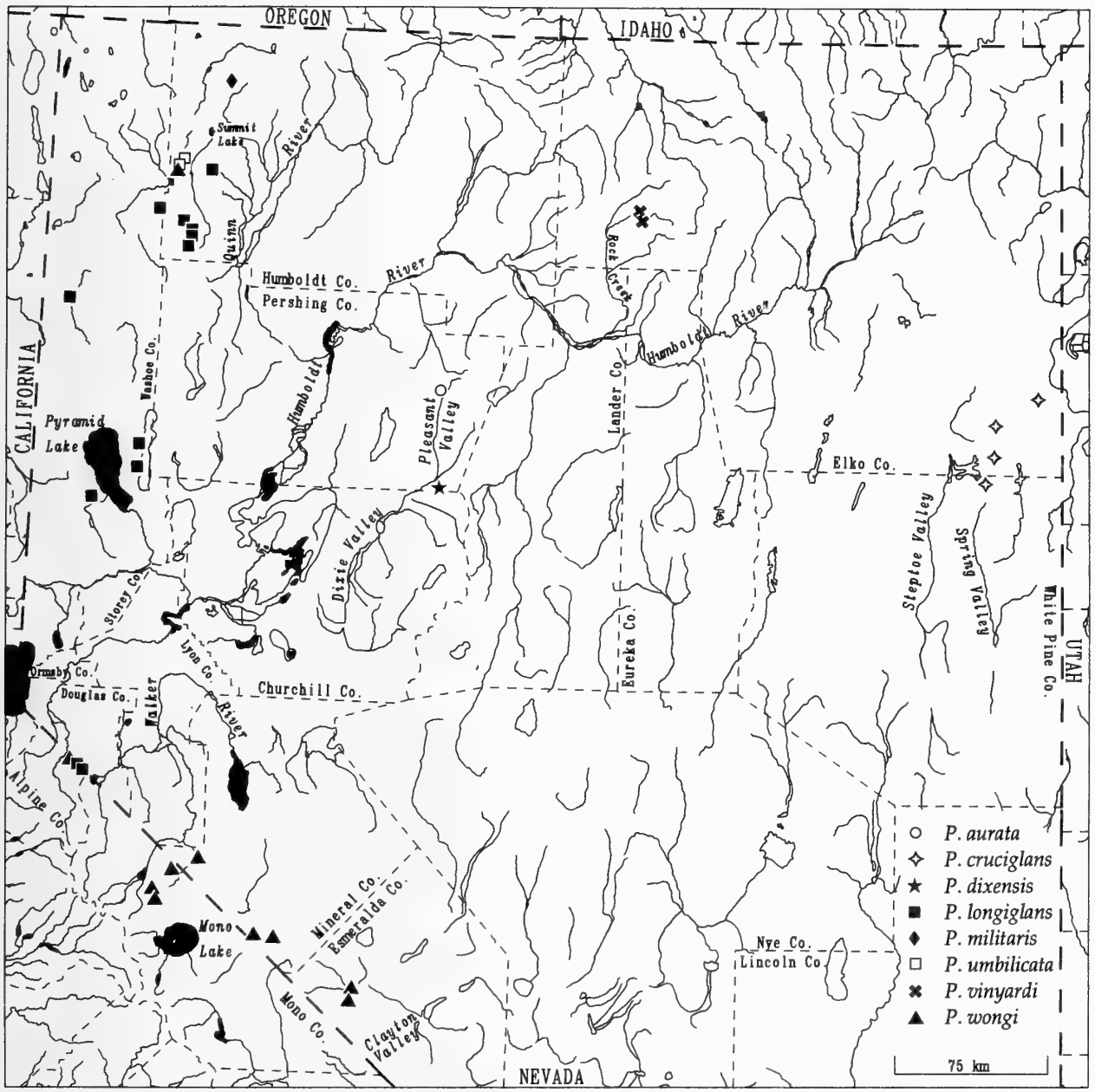


Figure 52

Map showing distributions of *Pyrgulopsis* species of isolated basins of Nevada and the Lahontan Basin. Previously known records for *P. wongi* are not shown. The distributions of *P.* ***limaria*** and *P.* ***notidicola,*** locally endemic species dwelling in very close proximity to *P.* ***umbilicata*** (in Mud Meadows), are not shown.

anterior edge at or near mid-line, slightly shorter to as long as bursa, medium width. Seminal receptacle small, pouchlike, overlapping or lateral to anteriormost bursa or proximal bursal duct.

Testis 1.25–1.5 whorls, filling more than 50% of digestive gland behind stomach, overlapping posterior and part of anterior stomach chamber. Prostate gland small, bean-shaped, pallial portion short, narrowly ovate in section. Proximal pallial vas deferens nearly straight or having a weak loop. Penis (Figure 46D, E) large; base rectangular, weakly folded or smooth; filament medium length and width, muscular, tapering to point; lobe short,

pointed, slightly oblique; sometimes nearly absent, with distal edge of penis rounded and slightly bulging. Terminal gland very small (often absent), dotlike, ventral. Penial duct straight, near outer edge.

Type locality: Crittenden Springs, Thousand Springs Creek, Elko County, Nevada, T. 42 N, R. 69 E, NE ¼ section 8 (Figure 56). Holotype, USNM 874724 (Figure 24G), collected by R. Hershler and P. Hovingh, 30 August 1992; paratypes, USNM 860722. The type locality is a shallow, broad (30 m) rheocrene flowing down a steep mountainside.

Remarks: *Pyrgulopsis* ***lentiglans*** differs from other endemic species of Thousand Springs drainage in its smaller size and strongly frilled operculum. This snail differs from these and other congeners of the region in having a small penial lobe bearing a very reduced (often absent) terminal gland.

Material examined: NEVADA. *Elko County:* Crittenden Springs, USNM 854639, USNM 860722, USNM 873327, USNM 874724.—Spring, southwest corner of Crittenden Reservoir, Thousand Springs Creek, T. 42 N, R. 69 E, SW ¼ section 17, USNM 854540.

Pyrgulopsis ***plicata*** Hershler, sp. nov.

Black Canyon pyrg

(Figures 10E, 13F, 24I, J, 46F, G)

Etymology: From *plicatus* (Latin), folded; referring to the basally folded penis characterizing this species.

Diagnosis: Medium-sized, with broadly to ovate conic shell. Penis medium-large; filament medium length, lobe short. Penial ornament a large Dg1.

Description: Shell (Figures 10E, 24I, J) broadly to ovate conic; width/height, 72–85%; height, 2.3–2.9 mm; width, 1.8–2.2 mm; whorls, 4.0–4.5. Protoconch 1.5 whorls, diameter 0.38 mm; initial 0.5–0.75 whorl very weakly wrinkled (mostly near inner edge), otherwise smooth. Teleoconch whorls medium to high convexity; shoulders absent to medium developed; body whorl often slightly disjunct and strongly translated behind the aperture. Aperture large, ovate, usually disjunct. Inner lip thick, without columellar shelf. Outer lip slightly thickened, orthocline or weakly prosocline, without sinuation. Umbilicus rimate to shallowly perforate. Periostracum light tan.

Operculum (Figure 13F) ovate, amber, nuclear region reddish; nucleus eccentric; dorsal surface very weakly frilled. Attachment scar thick all around.

Radula 740 × 100 μm, with 60 rows of teeth. Central tooth 26 μm wide, with medium to highly indented dorsal edge; lateral cusps, 4–7; central cusp broad, daggerlike; basal cusps medium-sized, sometimes accompanied by weak swelling to outside. Basal tongue broad V-shaped, basal sockets medium depth. Lateral tooth formula 3-1-3(4); neck weakly flexed; outer wing 150% of cutting edge length. Inner marginal teeth with 19–25 cusps; cutting edge occupying 38% of length of tooth. Outer marginal teeth with 24–30 cusps; cutting edge occupying 30% of length of tooth. Stomach longer than style sac; stomach chambers equal-sized; stomach caecum very small.

Cephalic tentacles medium to dark grey-brown or black. Snout light to dark grey-brown. Foot light to medium grey-brown. Opercular lobe black along outer edge; inner edge medium to dark grey-brown. Neck light to medium grey-brown. Pallial roof, visceral coil dark brown or black. Almost entire length of penial filament and distal penis, particularly portion near outer edge, medium to darkly pigmented.

Ctenidial filaments, 17; without pleats; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, positioned posterior to middle of ctenidium. Renal gland oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.5 whorl, filling less than 50% of digestive gland behind stomach, abutting posterior edge of stomach. Distal female genitalia shown in Figure 46F. Albumen gland having short or no pallial component. Capsule gland shorter, narrower than albumen gland, broadly ovate in section; rectal furrow weakly developed. Ventral channel slightly overlapping capsule gland; longitudinal fold weakly developed. Genital aperture a terminal pore, slightly raised, having short anterior extension. Coiled oviduct a tight, posterior-oblique loop. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, ovate, longitudinal, with 50% or less of length posterior to gland. Bursal duct originating from anterior edge at or near mid-line, 50% of length of bursa, narrow to almost as wide as bursa, duct sometimes shallowly embedded in albumen gland. Seminal receptacle small, overlapping or adjacent to anterior portion of bursa.

Testis 1.5 whorls, filling more than 50% of digestive gland behind stomach, overlapping posterior and part of anterior stomach chambers. Prostate gland small, bean-shaped, pallial portion short, narrowly ovate in section. Proximal pallial vas deferens having large, well-developed loop, sometimes weakly reflexed. Penis (Figure 46G) medium-large; base elongate-rectangular, proximal portion folded under remaining penis; inner edge folded; filament medium length, narrow or medium width, tapering to point, slightly oblique; lobe short, hemispherical, longitudinal. Dg1 large, narrow, raised; longitudinal (although proximal portion curves slightly across width of penis), borne along outer edge proximally. Penial duct straight, very close to outer edge.

Type locality: Spring, Black Canyon, East Fork Sevier River, Garfield County, Utah, T. 32 S, R. 2 W, NW ¼ section 11 (Figure 56). Holotype, USNM 883594 (Figure

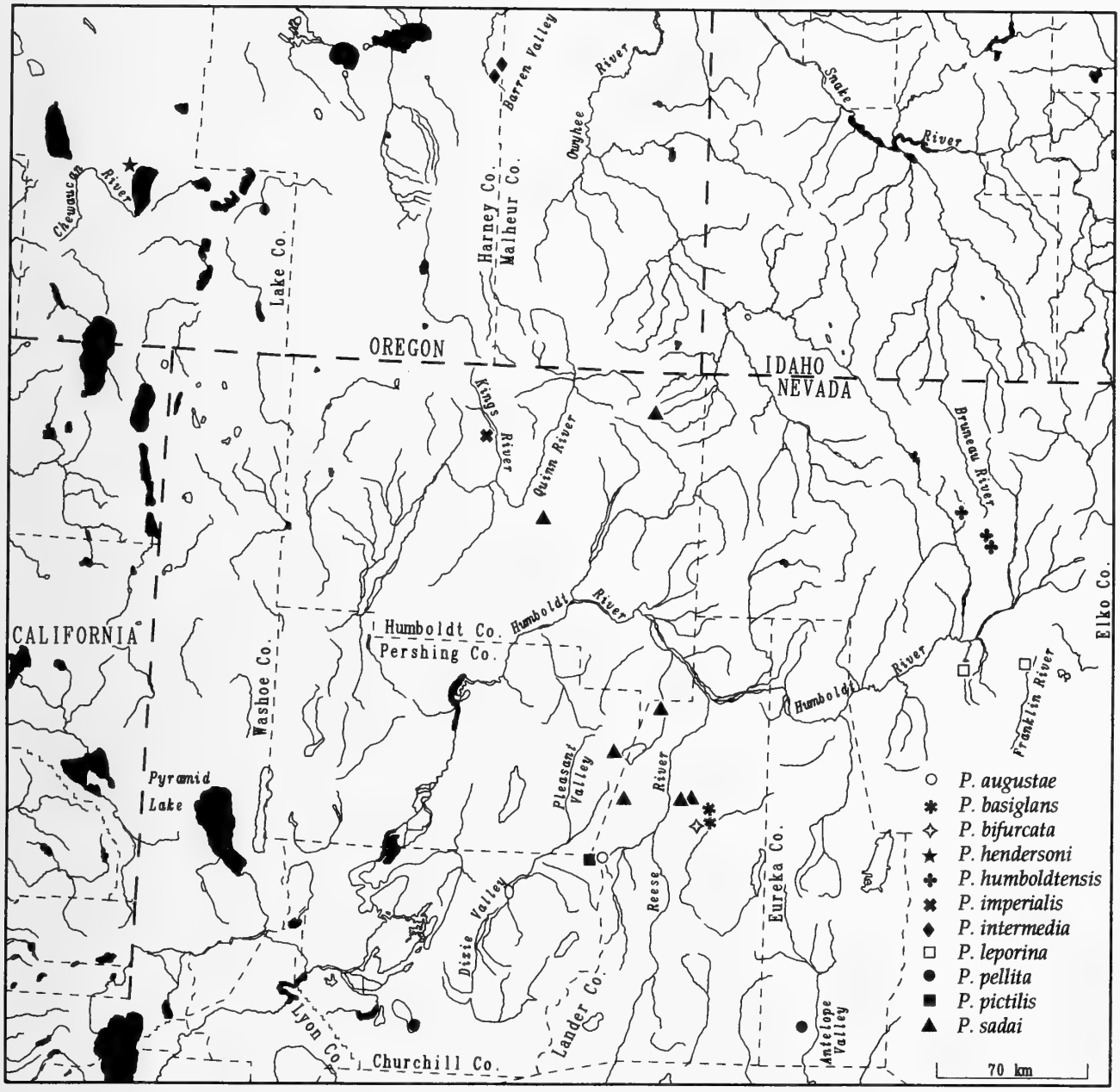


Figure 53

Map showing distributions of *Pyrgulopsis* species of the Lahontan Basin and the Oregon lakes region. Previously known records for *P. hendersoni* and *P. intermedia* are not shown. In cases where congeners are sympatric, symbols are slightly offset.

24I), collected by R. Hershler and P. Hovingh, 14 July 1993; paratypes, USNM 860727. The type locality is a series of small rheocrenes emerging from a steep hillside and feeding a reservoir.

Remarks: *Pyrgulopsis* ***plicata*** differs from other species of the Sevier River drainage in penial ornament, which consists solely of an elongate Dg1. *Pyrgulopsis* ***cruciglans,*** from eastern Nevada, has a similar pattern of ornament, although the gland is much larger and transversely positioned in this species.

Material examined: UTAH. *Garfield County:* Spring, Black Canyon, USNM 860727, USNM 883594.

*Pyrgulopsis **fusca*** Hershler, sp. nov.

Otter Creek pyrg

(Figures 10F, 24K–M, 47A–C)

Etymology: From *fuscus* (Latin), dark, swarthy; referring to the black body pigmentation characterizing this snail.

Diagnosis: Medium-sized, with ovate- to elongate-conic shell. Penis medium-sized; filament medium length; lobe short. Penial ornament of small terminal, penial, and ventral glands.

Description: Shell (Figures 10F, 24K–M) ovate- to elongate-conic, width/height, 61–73%; height, 2.5–4.4 mm; width, 1.6–2.9 mm; whorls, 4.25–5.25. Protoconch 1.5 whorls, diameter 0.40 mm; initial 0.75 whorl very weakly wrinkled (mostly near inner edge), otherwise smooth. Teleoconch whorls medium to high convexity, shoulders narrow to broad, sculpture including faint spiral striae; body whorl often slightly disjunct behind the aperture. Aperture ovate, adnate or slightly disjunct. Inner lip thin, sometimes having very narrow columellar shelf. Outer lip thin, slightly prosocline, without sinuation. Umbilicus rimate or shallowly perforate. Periostracum dark tan.

Operculum ovate, amber, nuclear region reddish; nucleus eccentric; dorsal surface weakly frilled. Attachment scar slightly thickened along inner edge and between nucleus and inner edge.

Radula 650 × 100 μm, with 50 rows of teeth. Central tooth 24 μm wide, with highly indented dorsal edge; lateral cusps, 3–8; central cusp medium width, spoonlike; basal cusps small, sometimes accompanied by slight thickenings to outside. Basal process V-shaped, basal sockets medium depth. Lateral tooth formula 2(3, 4)-1-3(4, 5); neck weakly flexed; outer wing 220% of cutting edge length. Inner marginal teeth with 21–28 cusps; cutting edge occupying 34% of length of tooth. Outer marginal teeth with 27–33 cusps; cutting edge occupying 28% of length of tooth. Stomach slightly longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles dark brown or black, with narrow unpigmented streak centrally. Snout, foot medium brown or black. Opercular lobe sometimes dark along inner edge and/or along outer edge. Neck light to medium grey-brown. Pallial roof, visceral coil dark brown or black. Penial filament darkly pigmented internally.

Ctenidial filaments, 19, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, centered well posterior to middle of ctenidium. Renal gland longitudinal; kidney opening slightly thickened. Rectum broadly overlapping pallial oviduct, slightly overlapping prostate gland.

Ovary 1.0–1.25 whorls, filling more than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 47A. Albumen gland having short pallial component. Capsule gland shorter, narrower than albumen gland, subcircular in section; rectal furrow medium depth. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct usually of two overlapping posterior-oblique loops; proximal loop lightly pigmented internally. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, ovate, longitudinal, with most of length posterior to gland. Bursal duct originating from anterior edge at mid-line, 50% to almost as long as bursa, medium width. Seminal receptacle medium-sized, pouch-like, curved or folded, overlapping anteriormost portion of bursa.

Testis 2.0 whorls, filling almost all of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland broad bean-shaped, pallial portion short, narrowly ovate in section. Proximal pallial vas deferens having well-developed, reflexed loop. Penis (Figure 47B, C) medium sized; base elongate-rectangular, inner edge weakly folded or smooth; filament medium length, broad, tapering to point, longitudinal or slightly oblique; lobe short, truncate, longitudinal. Terminal gland small, subcircular, distal, ventral. Penial gland small (sometimes reduced or absent), narrower than filament, positioned on filament near base. Ventral gland small, sub-circular or ovate (transverse), borne on low swelling, positioned near base of filament. Penial duct straight, near outer edge.

Type locality: Spring brook, Otter Creek, ca. 1.6 km above The Narrows, Piute County, Utah, T. 28 S, R. 1 W, SW ¼ section 17. Holotype, USNM 883439 (Figure 24K), collected by R. Hershler and P. Hovingh, 1 October 1993; paratypes, USNM 860728. The type locality is a small brook (2 cm deep, 1 m wide), fed by numerous small springs, which enters Otter Creek.

Remarks: This snail differs from similar *P. kolobensis* in its much narrower penis, with very reduced lobe, and weakly developed glands; and smaller, narrower bursa copulatrix. The distribution of this snail is shown in Figure 56.

Material examined: UTAH. *Piute County:* Spring brook, Otter Creek, USNM 860728, USNM 883439, USNM 883484. *Sevier County:* Burr Creek, Otter Creek drainage, T. 25 S, R. 1 W, SW ¼ section 26, USNM 883573, USNM 892028.—Spring, Little Lost Creek, Sevier River drainage, T. 24 S, R. 1 E, center section 18, USNM 883430, USNM 883442.

*Pyrgulopsis **chamberlini*** Hershler, sp. nov.

Smooth Glenwood pyrg

(Figures 10G, 25A–C, 47D–G)

Etymology: Named after the late Ralph V. Chamberlin, in recognition of his extensive fieldwork and taxonomic

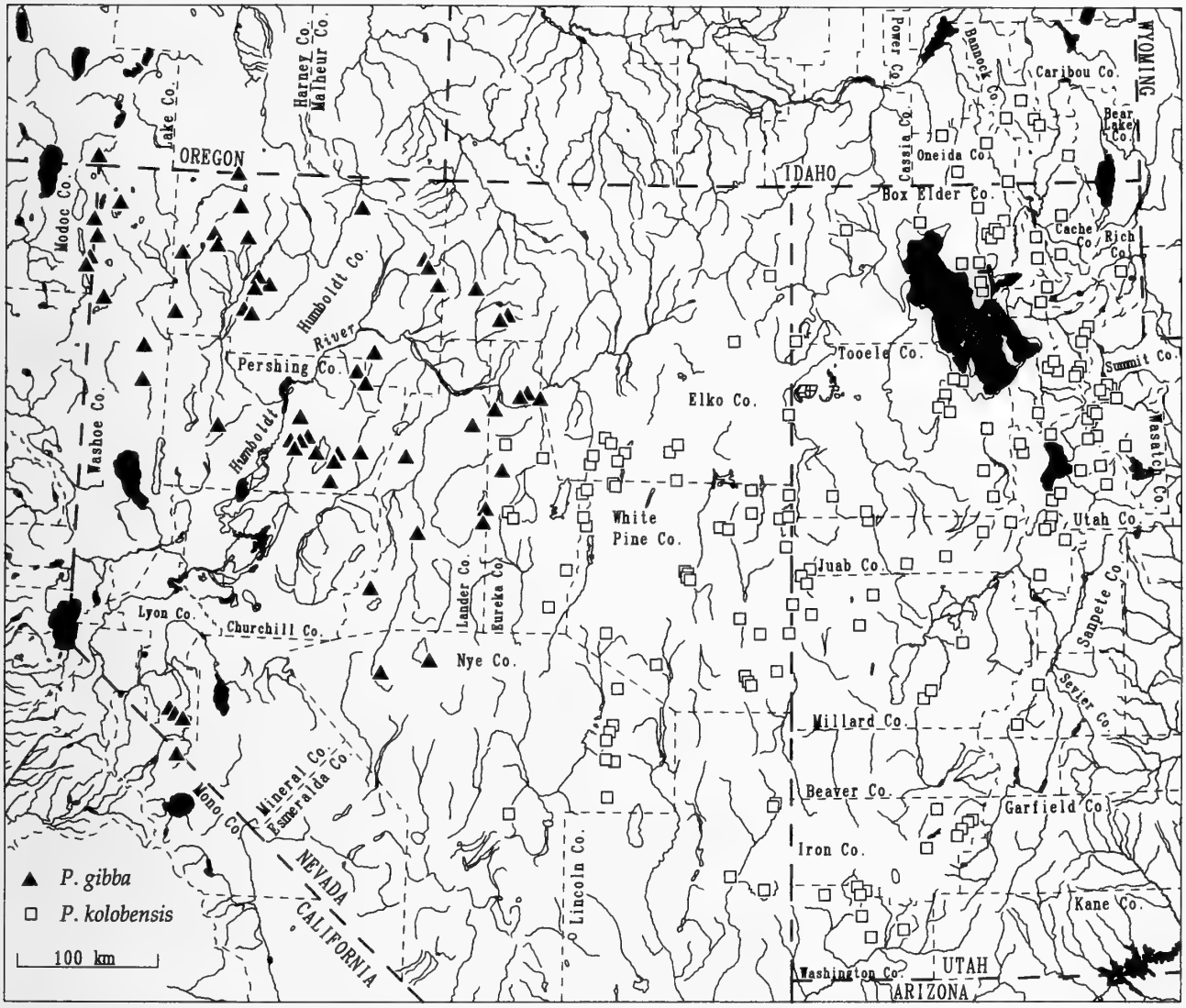


Figure 54

Map showing distributions of *P. gibba* and *P. kolobensis*. Previously known records for *P. gibba* are not shown.

studies pertaining to aquatic mollusks of the eastern Great Basin.

Diagnosis: Medium-sized to large, with ovate-conic shell. Penis large, filament medium length, lobe short. Penial ornament a medium-sized terminal gland, large penial gland, large Dg1, small Dg2, small Dg3 (sometimes absent), one to six additional dorsal glands, and small ventral gland.

Description: Shell (Figures 10G, 25A–C) ovate-conic, width/height, 64–78%; height, 2.3–4.3 mm; width, 1.8–3.1 mm; whorls, 4.5–6.0. Protoconch 1.25 whorls, diameter 0.33 mm; very weakly wrinkled at apex, otherwise smooth. Teleoconch whorls medium convexity, shoulders well developed, often having with broad shelf; body whorl often slightly disjunct behind the aperture. Aperture ovate, slightly disjunct in largest specimens. Inner lip slightly thickened, columellar shelf medium width. Outer lip usually thin, but slightly thickened in largest specimens, prosocline, without sinuation. Umbilicus absent or narrowly rimate. Periostracum light green.

Operculum ovate, amber, nuclear region reddish; nucleus eccentric; dorsal surface weakly frilled. Attachment scar thick all around, broadly so between nucleus and inner edge.

Radula 710 × 100 μm, with 62 rows of teeth. Central tooth 28 μm wide, with highly indented dorsal edge; lateral cusps, 4–6; central cusp narrow (sometimes long),

daggerlike; basal cusps medium-sized. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 2(3)-1-3(4); neck weakly flexed; outer wing 175% of cutting edge length. Inner marginal teeth with 26–30 cusps; cutting edge occupying 40% of length of tooth. Outer marginal teeth with 32–34 cusps; cutting edge occupying 25% of length of tooth. Stomach as long a style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented or light brown; proximal section unpigmented. Snout light to dark grey-brown. Foot light brown. Opercular lobe light grey along inner edge, sometimes all around. Neck very light grey. Pallial roof, visceral coil dark brown or black, sometimes uniformly pigmented. Penial filament darkly pigmented along almost entire length; distal base often similarly pigmented.

Ctenidial filaments, 18, weakly pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, centered posterior to middle of ctenidium. Renal gland oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.75–1.0 whorl, filling 50% of digestive gland behind stomach, abutting or slightly overlapping posterior stomach chamber. Distal female genitalia shown in Figure 47D. Albumen gland having medium-large (33% or more) pallial component. Capsule gland shorter, narrower than albumen gland, having distinct pigment patch alongside genital aperture, sub-globose in section; rectal furrow weak. Ventral channel broadly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal pore mounted on small papilla, having short anterior extension. Coiled oviduct of two overlapping, posterior-oblique loops, distal loop having dark pigmented streak. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix long, medium width, lying along ventral margin of gland, ovate, longitudinal, 50–75% of length posterior to gland. Bursal duct originating from anterior edge at mid-line, 50% of length of bursa, medium width. Seminal receptacle small, elongate pouch, rarely folded, overlapping anteriormost portion of bursa.

Testis 1.25 whorls, filling more than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Prostate gland large, elongate bean-shaped, pallial portion short, ovate in section. Proximal pallial vas deferens having well-developed, reflexed loop. Penis (Figures 47E–G) large; base rectangular, often elongate, smooth or weakly folded along inner edge, usually constricted proximally; filament medium length, narrow, gently tapering, oblique; lobe short, broadly rounded, longitudinal or slightly oblique. Terminal gland medium-sized, ovate, rarely bifurcate, usually transverse, ventral. Penial gland filling most of length of filament and small portion of base, almost as wide as filament. Dg1 large, narrow, raised on low pedicel, longitudinal (although proximal portion sometimes oblique), borne along outer edge proximally, rarely abutting the penial gland, sometimes accompanied along inner side by small, circular, raised gland. Dg2 small, ovate, distal. Dg3 small, ovate-elongate (sometimes dotlike or absent), slightly raised. Dorsal surface having one to six additional longitudinal glands proximal to Dg2, units usually dotlike or ovate, but also often including one to two elongate glands near inner edge. Ventral gland small, ovate, transverse, borne on low swelling, positioned near base of lobe; sometimes accompanied by dotlike or small, circular gland proximally. Penial duct straight, near outer edge.

Type locality: Spring, Glenwood, Sevier River drainage, Sevier County, Utah, T. 23 S, R. 2 W, NW ¼ section 36 (Figure 56). Holotype, USNM 883576 (Figure 25A), collected by R. Hershler and P. Hovingh, 15 July 1993; paratypes, USNM 860729. Two springs are found in a small drainage at Glenwood. An upper spring flows alongside HWY 119, while in a deeply entrenched area below, a second, more mineralized rheocrene emerges amongst a thicket of downed trees. The type locality is the lower spring, which was highly impacted by recreational activities. Note that this species also occurs in the upper spring and that *P. **inopinata,*** described next, also is present in both springs.

Remarks: This species is contrasted above with *P. **anguina,*** from Snake Valley.

Material examined: UTAH. *Sevier County:* Spring (lower), Glenwood, USNM 854786, USNM 860729, USNM 883576, USNM 883944.—Glenwood, FMNH 178389.—Spring (upper), Glenwood, Sevier River drainage, T. 23 S, R. 2 W, NW ¼ section 36, USNM 854784.

*Pyrgulopsis **inopinata*** Hershler, sp. nov.

Carinate Glenwood pyrg

(Figures 10H, 25D–F, 47H–J)

Etymology: From *inopinatus* (Latin), unexpected; referring to the investigator's surprise at discovering a carinate *Pyrgulopsis* along the Wasatch Front.

Diagnosis: Medium-sized, with ovate- to narrow-conic shell. Penis medium-sized, filament short, lobe medium length. Penial ornament a medium-sized terminal gland, large Dg1, small Dg2 (often absent), small Dg3, and medium-sized ventral gland.

Description: Shell (Figures 10H, 25D–F) ovate- to narrow-conic, width/height, 55–63%; height, 2.9–3.5 mm; width, 1.4–2.1 mm; whorls, 5.0–5.75. Protoconch 1.25 whorls, diameter 0.34 whorls, smooth or very weakly wrinkled at apex. Teleoconch whorls flat to medium convexity, without shoulders, sutures shallow; final 2.0 whorls usually having weak to well-developed peripheral angulation or narrow keel, sculpture sometimes weaker on body whorl; body whorl often slightly disjunct behind

the aperture. Aperture ovate, usually slightly disjunct. Inner lip thickened in larger specimens, without columellar shelf. Outer lip thin, orthocline or slightly prosocline, weakly sinuate. Umbilicus absent or rimate. Periostracum tan.

Operculum ovate, amber, slightly darker in nuclear region; nucleus eccentric; dorsal surface strongly frilled; outer margin having weak rim. Attachment scar strongly thickened all around.

Radula 610 × 105 μm, with 55 rows of teeth. Central tooth 29 μm wide, with medium indented dorsal edge; lateral cusps, 5–7; central cusp medium width, rounded or daggerlike; basal cusps small. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 3(4, 5)-1-4(5); neck weakly to medium flexed; outer wing 160% of cutting edge length. Inner marginal teeth with 23–27 cusps; cutting edge occupying 34% of length of tooth. Outer marginal teeth with 28–33 cusps; cutting edge occupying 27% of length of tooth. Stomach longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles medium grey to black, unpigmented around eyes. Snout medium grey to black. Foot light grey to black. Opercular lobe diffuse black along inner edge. Neck light grey. Pallial roof, visceral coil medium grey to black, pigment lighter along genital ducts. Penial filament black along almost entire length; pigment often extending onto distal penis.

Ctenidial filaments, 24, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, positioned slightly posterior to middle of ctenidium. Renal gland longitudinal, kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.75–1.0 whorl, filling less than 50% of digestive gland behind stomach, slightly overlapping posterior stomach chamber. Distal female genitalia shown in Figure 47H. Albumen gland having short pallial component. Capsule gland shorter, slightly narrower than albumen gland, broadly ovate in section; rectal furrow deep. Ventral channel slightly overlapping capsule gland; longitudinal fold small. Genital aperture a terminal pore mounted on a slightly muscular papilla, having short anterior extension. Coiled oviduct of two small, posterior-oblique loops; proximal portion sometimes only weakly kinked. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, ovate, longitudinal, with 50% of length posterior to gland. Bursal duct originating from anterior edge at mid-line, 50% of bursa length, medium width, often shallowly embedded in albumen gland. Seminal receptacle small, pouch-like, overlapping or lateral (ventral) to anterior portion of bursa.

Testis 1.5–2.0 whorls, filling more than 50% of digestive gland behind stomach, overlapping posterior and part of anterior stomach chambers. Prostate gland bean-shaped, pallial portion short, ovate in section. Proximal pallial vas deferens having well-developed, weakly reflexed loop. Penis (Figure 47I, J) medium-sized; base elongate-rectangular, folded; filament short, narrow, tapering to point, longitudinal; lobe longer (sometimes considerably so) than filament, rectangular, longitudinal. Terminal gland medium-sized, ovate, transverse, largely ventral. Dg1 elongate, extending from middle of penis base near outer edge onto proximal half of filament, almost as wide as filament, slightly raised; longitudinal, but with proximal-most portion slightly oblique. Dg2 small, circular, absent in about 50% of specimens, positioned near inner edge of lobe. Dg3 small, ovate, positioned along outer edge of lobe. Ventral gland medium-sized, ovate, borne on low swelling, transverse-oblique, positioned near base of lobe. Penial duct straight, near outer edge.

Type locality: Spring, Glenwood, Sevier River drainage, Sevier County, Utah, T. 23 S, R. 2 W, NW ¼ section 36 (Figure 56). Holotype, USNM 883943 (Figure 25D), collected by R. Hershler and P. Hovingh, 10 May 1995; paratypes, USNM 860730. The type locality is the upper spring at Glenwood (see above), which flows out of a pipe and forms a shallow brook.

Remarks. Recent carinate species of *Pyrgulopsis* have previously been recorded only in the western Lahontan and Klamath Lake basins (*P. nevadensis, P. archimedis* Berry, 1947, respectively; Taylor, 1960:fig. 1). The penial ornament of *Pyrgulopsis* ***inopinata*** is substantially different than that shared by the above species (see Hershler, 1994), as well as that of *P.* ***carinata*** from southeastern Nevada (described above), and instead suggests affinity with the group of snails having an elongate, distal Dg1. Among members of this group, *P.* ***inopinata*** most closely resembles species from Snake River drainage (*P. robusta*) and Oregon Lakes (*P. hendersoni*), but differs in its smaller size and carinate shell.

At a second, nearby site south of Sigurd, the typical narrow-carinate form of this species is found along with a smooth, ovate-shelled snail. The nature of this variation is as yet unclear—one possibility is that this species may be hybridizing with *P. kolobensis,* which occurs in a typical form in a spring only 3 km to the north.

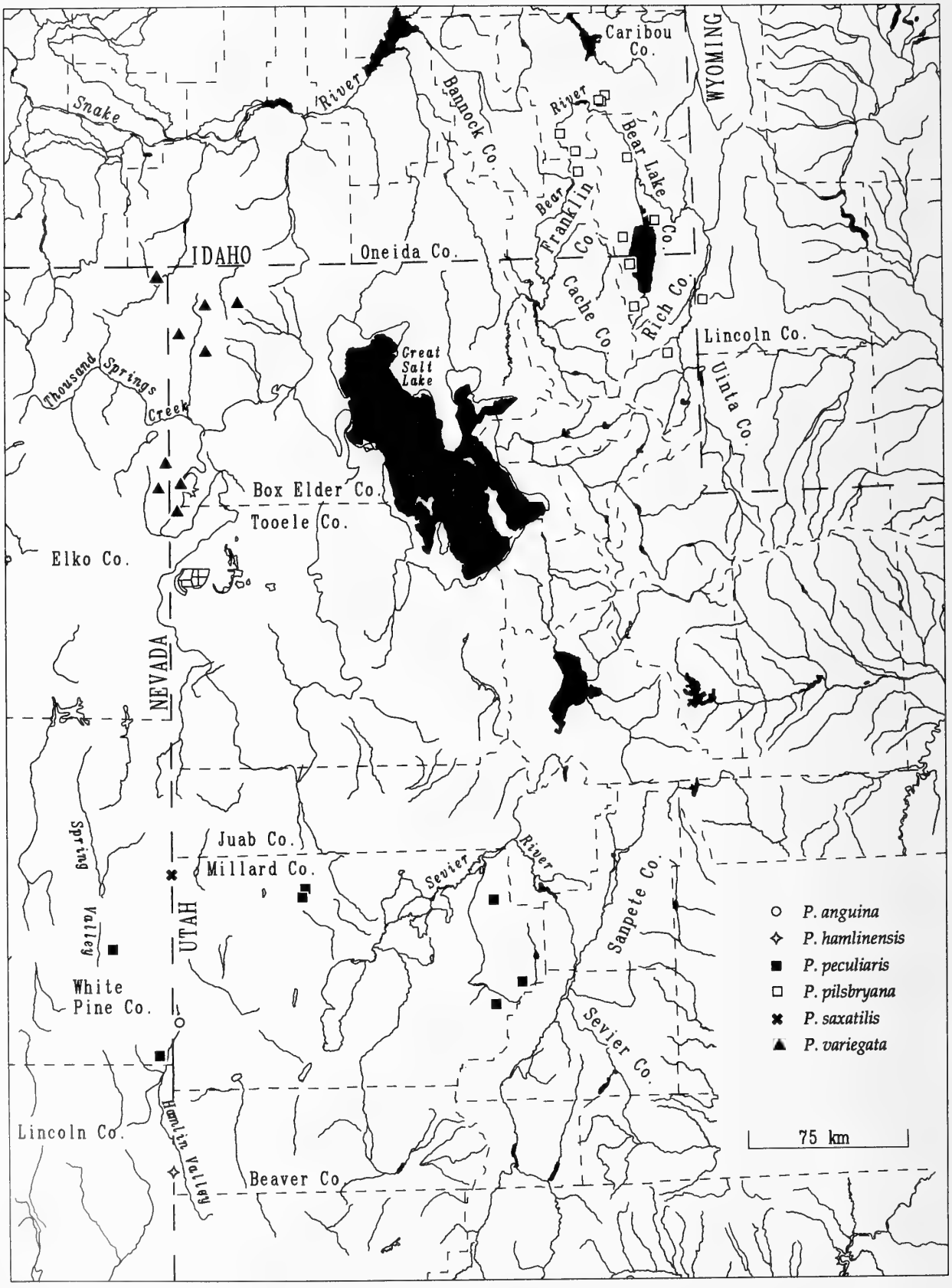
Material examined: UTAH. *Sevier County:* Spring (upper), Glenwood, USNM 854783, USNM 860730, USNM 883943.—Spring (lower), Glenwood, USNM 854785, USNM 883886.—Spring, 5.4 km south of Sigurd, Sevier River drainage, T. 23 S, R. 2 W, SW ¼ section 14, USNM 883942, USNM 892032, USNM 892033.

Pyrgulopsis ***nonaria*** Hershler, sp. nov.

Ninemile pyrg

(Figures 10I, 25G, 48A–C)

Etymology: From *nonarius* (Latin), of the ninth; referring to endemism of this species in the vicinity of Ninemile Reservoir, Utah.


Caribou Co.
WYOMING
Snake River
Bannock Co.
Bear River
Bear Lake Co.
Franklin Co.
Cache Co.
Rich Co.
IDAHO
Oneida Co.
Lincoln Co.
Uinta Co.
Great Salt Lake
Thousand Springs Creek
Box Elder Co.
Tooele Co.
Elko Co.
NEVADA
Juab Co.
Millard Co.
Sevier River
Sanpete Co.
Sevier Co.
Spring Valley
UTAH
White Pine Co.
Lincoln Co.
Hamlin Valley
Beaver Co.
P. anguina
P. hamlinensis
P. peculiaris
P. pilsbryana
P. saxatilis
P. variegata
75 km

Diagnosis: Medium-sized, with ovate- to narrow-conic shell. Penis large, filament and lobe short. Penial ornament of large terminal and ventral glands.

Description: Shell (Figure 10I, 25G) ovate- to narrow-conic; width/height, 60–71%; height, 2.5–2.9 mm; width, 1.6–1.9 mm; whorls, 4.5–5.0. Protoconch 1.25–1.3 whorls, diameter 0.35 mm; very weakly wrinkled at apex, otherwise smooth. Teleoconch whorls medium convexity, shoulders medium development; body whorl often slightly disjunct behind the aperture. Aperture ovate; usually disjunct. Inner lip slightly thickened, without columellar shelf. Outer lip thin, prosocline. Umbilicus shallowly perforate. Periostracum tan.

Operculum ovate, dark amber; nucleus eccentric; dorsal surface weakly frilled; outer margin having weak rim. Attachment scar thick all around.

Radula 750 × 120 μm, with 57 rows of teeth. Central tooth 32 μm wide, with medium indented dorsal edge; lateral cusps, 6–7; central cusp broad, daggerlike; basal cusps medium-sized. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 3(4)-1-3(4, 5); neck weakly flexed; outer wing 170% of cutting edge length. Inner marginal teeth with 23–33 cusps; cutting edge occupying 39% of length of tooth. Outer marginal teeth with 29–39 cusps; cutting edge occupying 29% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented to dark brown. Snout light to medium brown. Foot unigmented to light brown. Opercular lobe usually dark brown-black all around. Neck pigmented with scattered grey-brown granules. Pallial roof, visceral coil dark brown-black, pigment often uniform. Penial filament darkly pigmented along most of length.

Ctenidial filaments, 16, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, centered well posterior to middle of ctenidium. Renal gland oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.5–0.75 whorl, filling less than 50% of digestive gland behind stomach, slightly overlapping posterior stomach chamber. Distal female genitalia shown in Figure 48A. Albumen gland having short pallial component. Capsule gland shorter, narrower than albumen gland, subglobose in section; rectal furrow medium depth. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a broad, terminal slit having short anterior extension. Coiled oviduct a posterior-oblique loop sometimes preceded by weak twist or (overlapping) small posterior-oblique coil; coiled portion usually having narrow, light pigment band. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, ovate or sub-globular, longitudinal, with 33–60% of length posterior to gland; anterior portion sometimes slightly overlapped by gland. Bursal duct originating from anterior edge at mid-line, medium length and width. Seminal receptacle medium-sized, pouchlike, overlapping anterior half of bursa.

Testis 1.5 whorls, filling more than 50% of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland bean-shaped, pallial portion short, ovate in section. Proximal pallial vas deferens having well-developed loop. Penis (Figure 48B, C) large; base elongate-rectangular, smooth; filament short, narrow, tapering to point, usually oblique; lobe as long as filament, broad, clublike, longitudinal. Terminal gland large, narrow, slightly curved, transverse, largely ventral. Distal penis bearing two glandular dots (conforming to Dg2) in single specimen. Ventral gland large, narrow, transverse, borne on prominent swelling, positioned near base of lobe, sometimes accompanied distally by small, circular unit (also borne on swelling). Penial duct straight, near outer edge.

Type locality: Spring, east side of Ninemile Reservoir, Sanpete Valley, San Pete County, Utah, T. 19 S, R. 2 E, NW ¼ section 9 (Figure 56). Holotype, USNM 883566 (Figure 25G), collected by R. Hershler and P. Hovingh, 15 July 1993; paratypes, USNM 860731. The type locality is a shallow, broad, mineralized (1213 micromhos/cm) rheocrene emptying into Ninemile Reservoir.

Remarks: This species is similar to *P. kolobensis* in many details, but differs in consistently lacking a penial gland. Among the group of species having penial ornament consisting solely of terminal and ventral glands, *Pyrgulopsis* ***nonaria*** and *P.* ***transversa*** (described below), which occurs in the northern portion of SanPete Valley, are distinctive in sharing a relatively narrow shell. These species differ in that *P.* ***nonaria*** has a shorter penial filament, larger ventral gland, and a more posteriorly positioned seminal receptacle.

Material examined: UTAH. *San Pete County:* Spring, east side of Ninemile Reservoir, USNM 860731, USNM 874376, USNM 883566.—Spring, northeast of Ninemile Reservoir, T. 19 S, R. 2 E, center section 4, USNM 874377.

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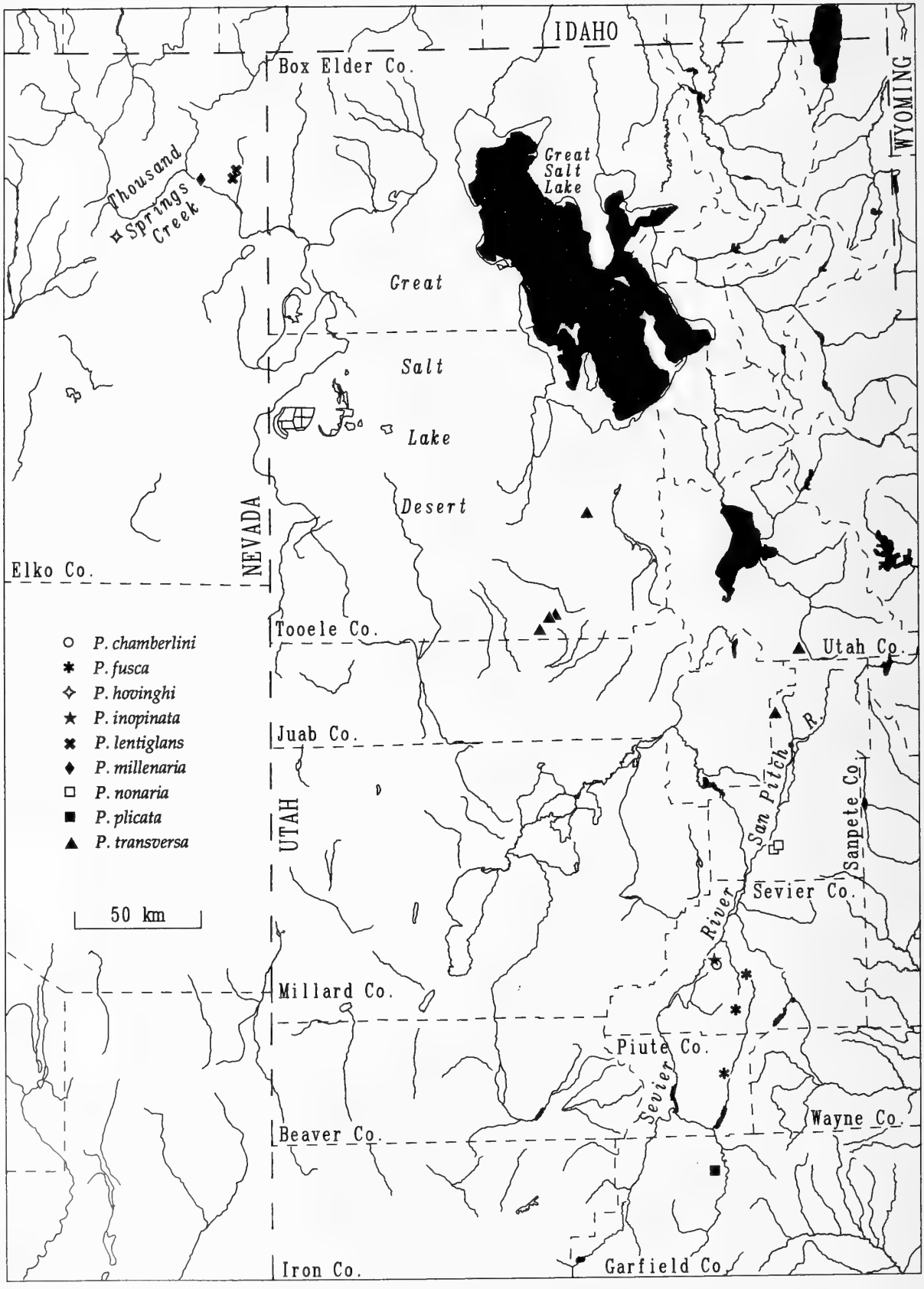
Figure 55

Map showing distributions of *Pyrgulopsis* species of the Bonneville Basin. Previously known records for *P. pilsbryana* are not shown.


IDAHO
WYOMING
Box Elder Co.
Thousand Springs Creek
Great Salt Lake
Great Salt Lake Desert
NEVADA
Elko Co.
Tooele Co.
Utah Co.
Juab Co.
UTAH
Millard Co.
Beaver Co.
Iron Co.
Piute Co.
Sevier Co.
Sanpete Co.
San Pitch R.
Sevier River
Wayne Co.
Garfield Co.
P. chamberlini
P. fusca
P. hovinghi
P. inopinata
P. lentiglans
P. millenaria
P. nonaria
P. plicata
P. transversa
50 km

Pyrgulopsis ***transversa*** Hershler, sp. nov.

Southern Bonneville pyrg

(Figures 10J, 16G–I, 25H–K, 48D–H)

Etymology: From *transversus* (Latin), crosswise; referring to the east-west distribution of this species, which cuts across several southern drainages in the Bonneville Basin.

Diagnosis: Medium-sized, with ovate- to narrow-conic shell. Penis medium-large, filament and lobe medium length. Penial ornament a small-medium terminal gland and small ventral gland (often absent).

Description: Shell (Figures 10J, 25H–K) ovate- to narrow-conic, width/height, 58–78%; height, 2.0–3.1 mm; width, 1.3–2.2 mm; whorls, 4.25–5.25. Protoconch 1.4–1.5 whorls, diameter 0.35 mm; weakly wrinkled along inner edge of initial 0.5 whorl, otherwise smooth. Teleoconch whorls low to medium convexity, shoulders weak to medium; body whorl often slightly disjunct behind the aperture. Aperture ovate, usually disjunct. Inner lip thick, with narrow to medium columellar shelf. Outer lip thin, prosocline, without sinuation. Umbilicus rimate or shallowly perforate. Periostracum tan or light brown.

Operculum ovate, amber, nuclear region reddish; nucleus eccentric; dorsal surface very weakly frilled; outer margin sometimes having very weak rim. Attachment scar sometimes slightly thickened along inner edge and between inner edge and nucleus.

Radula (Figure 16G–I) 650 × 110 μm, with 53 rows of teeth. Central tooth 26 μm wide, with highly indented dorsal edge; lateral cusps, 4–5; central cusp medium width, daggerlike; basal cusps small. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 2(3)-1-3; neck straight or weakly flexed; outer wing 160% of cutting edge length. Inner marginal teeth with 20–22 cusps; cutting edge occupying 37% of length of tooth. Outer marginal teeth with 28–34 cusps; cutting edge occupying 29% of length of tooth. Stomach longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented to light grey-brown. Snout unpigmented to medium grey-brown. Foot light to medium grey-brown. Opercular lobe black along inner edge, sometimes all around. Neck having scattered black granules. Pallial roof, visceral coil black, often uniformly pigmented. Penial filament usually lightly pigmented on proximal half; penis occasionally unpigmented.

Ctenidial filaments, 17, weakly pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, positioned posteriorly. Renal gland longitudinal or slightly oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.75 whorl, filling less than 50% of digestive gland behind stomach, slightly overlapping posterior stomach chamber. Distal female genitalia shown in Figure 48D. Albumen gland having short or no pallial component. Capsule gland shorter, narrower than albumen gland, ovate in section; rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit, sometimes weakly raised, having short anterior extension. Coiled oviduct usually of two small, overlapping posterior-oblique loops (proximal portion sometimes only twisted or kinked); distal loop usually having narrow band of light epithelial pigment. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, ovate-elongate, longitudinal, with 67–80% of length posterior to gland, anterior portion sometimes slightly overlapped by gland. Bursal duct originating from anterior edge at or slightly lateral to midline, medium length and width. Seminal receptacle small, pouchlike, overlapping proximal bursal duct.

Testis 1.5–2.0 whorls, filling almost all of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland very small, bean-shaped, entirely visceral, narrowly ovate in section. Proximal pallial vas deferens having well-developed bend. Penis (Figure 48E–H) large; base rectangular, smooth; filament medium length and width, gently tapering to point, slightly oblique; lobe medium length, slightly narrower than base, clublike, longitudinal. Terminal gland small-medium, circular-narrow, longitudinal-transverse, ventral. Glandular smear seen on base of filament in single specimen. Similar smear conforming to distal Dg2 seen in single specimen. Ventral gland small, circular-ovate, often absent, borne near base of lobe on low swelling. Penial duct straight, near outer edge.

Type locality: Sixmile Springs, Simpson Mountains, Old River Bed, Tooele County, Utah, T. 10 S, R. 8 W, NW ¼ section 33. Holotype, USNM 883221 (Figure 25H), collected by R. Hershler and P. Hovingh, 12 May 1993; paratypes, USNM 860732. The type locality is a series of small, mineralized (1126 micromhos/cm) springs at about 1778 m elevation. The spring sampled is a small "rheocrene" issuing out of a pipe (Figure 3D).

Remarks: This species is contrasted with *P.* ***nonaria***

←

Figure 56

Map showing distributions of *Pyrgulopsis* species of the Bonneville Basin. In cases where congeners are sympatric, symbols are slightly offset.

above. The distribution of this species is shown in Figure 56.

Material examined: UTAH. *Sanpete County:* Spring, west-northwest of Fountain Green, San Pete Valley, T. 14 S, R. 2 E, NW ¼ section 2, USNM 873333, USNM 883597. *Tooele County:* Sixmile Springs, Old River Bed (Figure 3D), USNM 860732, USNM 883221.—Indian Springs, Simpson Mountains, Old River Bed, T. 10 S, R. 8 W, NE ¼ section 3, USNM 883422.—Spring, Lee Creek, Government Creek drainage, Dugway Valley, T. 9 S, R. 8 W, SW ¼ section 36, USNM 883481.—Springs, Clove Creek, Rush Valley, T. 5 S, R. 6 W, NW ¼ section 32, USNM 883210. *Utah County:* Spring, Thistle Creek, Utah Lake drainage, T. 11 S, R. 3 E, SW ¼ section 12, USNM 883572.

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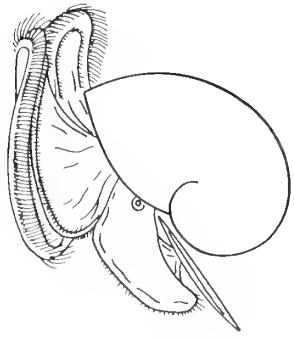

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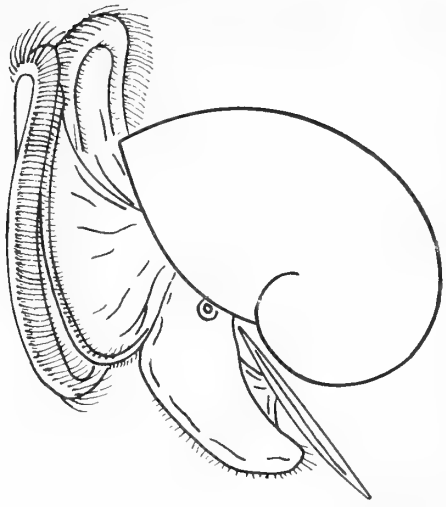

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Embryonic Shell Formation in the Scallop *Pecten maximus* (Linnaeus)

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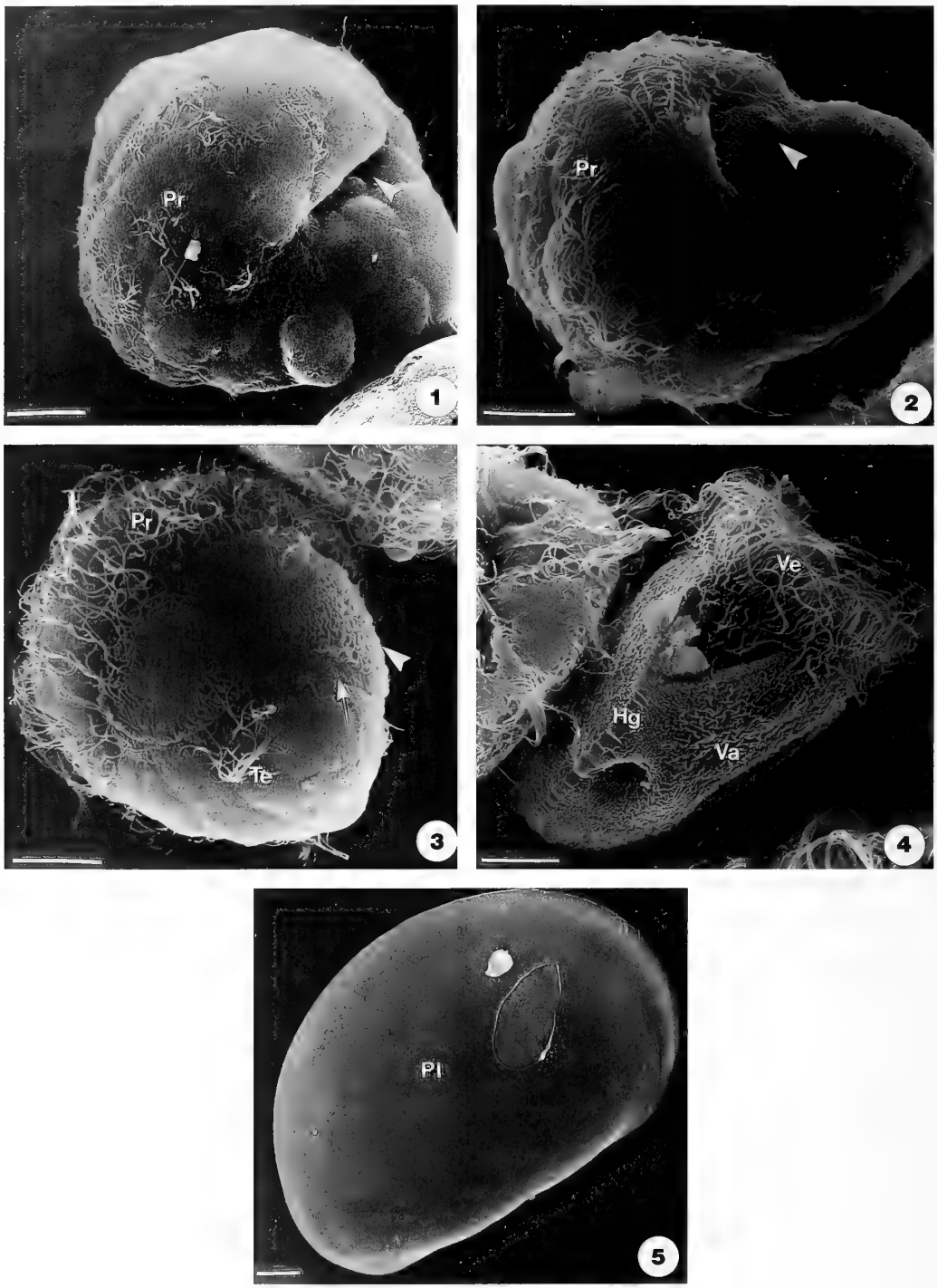
Abstract. Shell secretion during embryogenesis is described for the scallop *Pecten maximus.* Larval shell elaboration is preceded by an invagination of part of the dorsal epithelium termed shell field invagination or SFI. The first shell pellicle appears when the young larvae are only 20 h old (at 18–19°C incubation). This shell pellicle spreads rapidly over the larval body and by 45 h post-fertilization (at 18–19°C incubation), the shell or prodissoconch I surrounds the entire larval body. Prodissoconch I is calcified and D-shaped, and is classically referred to as the D-veliger stage. An ultrastructural examination indicates that the first shell pellicle is secreted by the cells which form the SFI pore, termed secreting cells. Microvilli-bearing cells are observed adjacent to the secreting cells and are referred to as microvilli cells. Cytoplasmic expansions originating from the microvilli cells cover and protect the recently secreted pellicle. The SFI invagination is formed by cells called proximal cells. These latter cells progressively evaginate during larval development and become the epithelial cells of the mantle. At the young veliger stage, the proximal cells adjacent to the secreting ones, termed proximal cells @, arch upward and become the outer cells of the mantle outer fold. At the D-veliger stage, the distal part of the secreting cells curve down and sink the newly formed pellicle into the intercellular space of the secreting and microvilli cells. This process leads to the formation of the periostracal groove. In the 45 h D-veliger of *P. maximus,* the shell pellicle is then secreted in the periostracal groove by the inner cells (secreting cells) of the outer fold of the mantle edge.

INTRODUCTION

In mollusks, shell formation is initiated during embryogenesis. To date, an extensive amount of literature has been generated which deals with the initation of shell secretion (for review, see Kniprath, 1981). Numerous papers describe a similar scheme for shell elaboration, and it is generally accepted that shell production is preceded by invagination of part of the dorsal ectoderm of the larva. This invagination has been called the shell gland by early workers (Ganin, 1873; Lankester, 1873). Thus, invagination of the ectoderm is followed by evagination of the shell gland and spreading of the secreted shell pellicle. Many authors consider that the shell gland is responsible for secretion of the first shell pellicle. Eyster (1983), however, indicated that no secretory function has been demonstrated for the shell gland. Conversely, shell secreting cells have been clearly identified in the gastropod *Aeolidia papillosa* by Eyter (1983). This last author used the terms "shell field" to describe the entire shell secreting epithelium and "shell field invagination" to refer to the shell gland.

Larval shells consist of two organic components: the periostracum and a matrix which contains the mineral crystallites (Wilbur & Simkiss, 1968). During shell formation, a thin organic pellicle first appears which allows the organic matrix to be deposited. According to Cather (1967) and Humphreys (1969), the first pellicle secreted becomes the periostracum, whereas for Kniprath (1972) it corresponds to the outer layer of periostracum.

In marine bivalves, the shell produced during embryogenesis is termed the prodissoconch I. Humphreys (1969) examined the initiation of the shell formation in *Mytilus edulis.* Kniprath (1979a) studied secretion of the shell in *Mytilus galloprovincialis* and Eyster & Morse (1984) localized the first shell material in *Spisula solidissima.* Few



Explanation of Figures 1 to 5

Figure 1. Young trochophore 15 h post-fertilization. The SFI (arrow head) is tranversally elongated and localized in the post-trochal dorsal region; (Pr) prototroch. SEM. Scale bar = 10 μm. Figure 2. 20 h trochophore. First organic material (arrow head) observed, and thin undulating pellicle seen at the surface of the SFI; (Pr) prototroch. SEM. Scale bar = 10 μm. Figure 3. 23 h trochophore. Shell pellicle (arrow head) spreads laterally over larval body. It is surrounded by a thick border (arrow) corresponding to the limit of the shell field; (Pr) prototroch; (Te) telotroch. SEM. Scale bar = 10 μm. Figure 4. Young veliger 30 h old. Shell pellicle is still undulated. The shell has two valves (Va) and presents a well-marked hinge (Hg); (Ve) velum. SEM. Scale bar = 10 μm. Figure 5. 45 h D-veliger. Shell surrounds the entire larval body and is the smooth calcified prodissoconch I (PI). SEM. Scale bar = 10 μm.

studies have examined the embryonic shell development in marine bivalves from an ultrastructural point of view.

The aim of this study was therefore to describe the development of the embryonic shell in the scallop *Pecten maximus*. Shell formation was examined from the development of shell field invagination to the prodissoconch I stage using SEM and TEM. Eyster's terminology (1983) for shell field invagination (SFI) is used in this paper.

MATERIALS AND METHODS

Adult scallops were collected from April to July in the Bay of Brest (France) and kept overnight in tanks with a continous flow of seawater (11°C). Scallops were then placed in spawning tanks with filtered seawater (1 μm) and warmed from 11°C to 18°C over a 2 hour period. Scallops that released oocytes were rapidly isolated to avoid autofertilization. Eggs were fertilized by addition of sperm at a ratio of five spermatozoa to one oocyte (Gruffydd & Beaumont, 1970). One hour post fertilization, eggs were passed through a 135 μm screen to remove any clumped eggs and then filtered onto a 25 μm screen and rinsed with filtered seawater (1 μm) to remove excess sperm. Embryos were then incubated in 201 tanks at a density of 50 embryos per ml in standing filtered seawater (1 μm) at 18–19°C. From the oocyte to the D-veliger stage (45 hours post-fertilization), samples (1000 embryos per sample) were collected through a 25 μm screen and rinsed with glutaraldehyde (2.5% in 0.2 M cacodylate buffer, adjusted with NaCl to 1100 mOsm, pH 7.25 for 2 hours). Embryos were subsequently transferred to tubes, fixed 1 hour at 4°C with glutaraldehyde and then rinsed twice in cacodylate buffer. Approximately 100 embryos were treated for scanning electron microscopy (SEM). Samples were dehydrated in a graded ethanol series, dried using CO_2 in a critical point apparatus, gold coated and then observed using a JEOL scanning electron microscope. The remaining embryos were post-fixed in 1% osmium tetroxide in 0.2 M cacodylate buffer for 1 h30, rinsed in buffer, dehydrated in a graded ethanol series and placed in a mixed medium Spurr's resin/ethanol 100° (v/v) (Spurr, 1969) for 6 hours. Samples were then impregnated in the same resin for 12 hours and finally embedded in Spurr's resin. Thin sections (60 nm) were mounted on 300 mesh grids, contrasted with uranyl acetate and lead citrate (Reynolds, 1963), and examined using a JEOL 100CX transmission electron microscope.

RESULTS

SEM observations are used to visualize formation of the embryonic shell in *P. maximus*. The SFI formation is the first event to be observed in *P. maximus*. This structure is seen when the larva is an early trochophore. Thus, 15 h post-fertilization, the ectodermal invagination (SFI) is seen on the dorsal side of the larva, beneath the prototroch. The SFI pore is elongated transversally (Figure 1).

The first organic material is observed at 20 h. This material can be visualized as a small circular undulating pellicle which covers the SFI (Figure 2).

Twenty-three hours after fertilization, the shell pellicle is a single structure which spreads laterally over the larval body. Observed from the dorsal region, the shell is "saddle-shaped." The secreted pellicle is surrounded by a rim corresponding to the limit of the shell field. Polarized microscopy indicates that shell is not calcified (Figure 3).

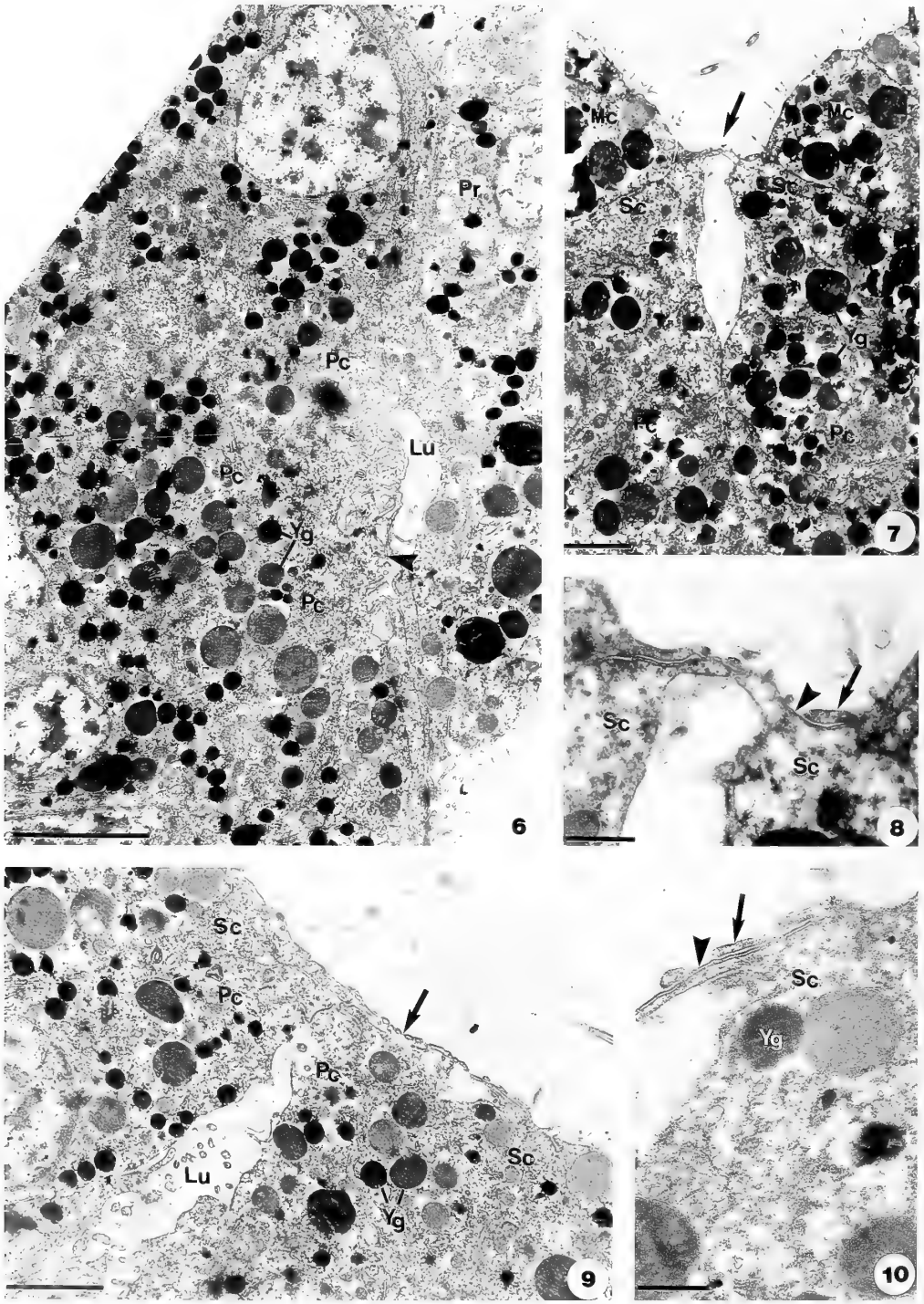
At the veliger stage, 30 h post-fertilization, the shell covers the larval body with the exception of the velum and the posterior region. At this time, the shell is paired, undulated, and possesses a hinge line (Figure 4).

After 45 h, the larval shell is the straight hinge line, prodissoconch I. It is smooth, calcified, and surrounds the entire body of the larva (Figure 5). Mineralization is detected near the hinge line and shell margins.

In addition to the SEM observations, an ultrastructural examination of the embryonic shell formation was performed by TEM. Twenty hours post-fertilization, a longitudinal section through an early trochophore indicates that the SFI is made up of undifferenciated cells which contain many yolk granules. These cells are termed proximal cells. This term indicates their position directly around the lumen of the SFI. The SFI lumen is lined with microvilli (Figure 6). In transverse section, the pore of the invagination is observed to be made up of microvilli-bearing cells. The microvilli join and cover the SFI opening. Adjacent to the pore cells and opposite the invagination, one can observe another type of microvilli-bearing cells (Figure 7). Part of the microvilli of this last type of cell are applied on the microvilli of the pore cells. The first shell organic material is secreted between the microvilli of the two kinds of cells. The cells forming the pore are responsible for the secretion of the pellicle; they are termed secreting cells. The other type of cells possessing microvilli are termed microvilli cells. The pellicle is formed at the apex of the secreting cells (Figure 8). Rapidly, the secreted pellicle extends across the aperture of the SFI while the proximal cells begin to reach the surface of the embryo (Figure 9). During its extension, the recently formed pellicle is always covered by the microvilli originating from the microvilli cells (Figure 10).

The localization of the differents kinds of cells mentioned above is outlined in Figure 11, drawn after Figure 9.

The proximal cells possess a well-developed ergastoplasm (Figure 12). The secreting cells have an elongated, basal nucleus, and their cytoplasm contains numerous RER citernae (Figure 12). The newly formed pellicle curves down between the secreting and the microvilli cells (Figure 13). The apical region of the secreting cells possesses an intracellular space situated between the cytoplasm and the shell pellicle (Figures 13, 14). This space contains numerous elecrodense granules. Abundant er-



Explanation of Figures 6 to 10

Figure 6. Longitudinal section through SFI of a 20 h trochophore. SFI made up of few differentiated cells, proximal cells (Pc); the invagination is lined with microvilli (arrow head); (Lu) SFI lumen; (Pr) prototroch; (Yg) yolk granules. TEM. scale bar = 4 μm. Figure 7. Cross section through SFI of a 20 h larva. SFI pore is formed by microvilli-bearing cells (Sc); the neighboring cells of the latter also bear microvilli; they are called microvilli cells (Mc). The cytoplasmic extensions of the two kinds of cells join at SFI pore aperture (↓); (Pc) proximal cells, (Yg) yolk granules. TEM. Scale bar = 2 μm. Figure 8. High magnification of microvilli of secreting and microvilli cells showing the first organic shell material elaborated (arrow head) at the secreting cells apex (Sc) and covered by the

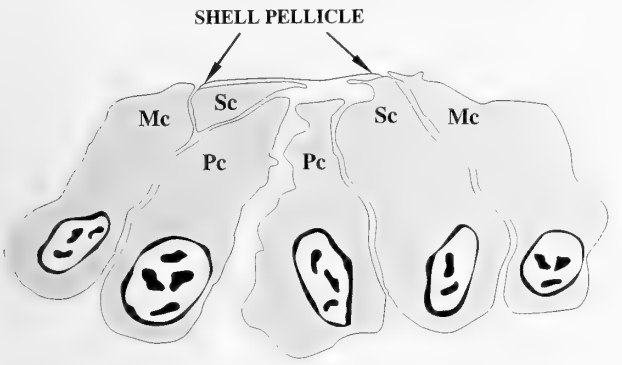


Figure 11

Cross section through SFI showing the cells involved in first larval shell formation in *Pecten maximus*; (Mc) microvilli cells; (Pc) proximal cells; (Sc) secreting cells.

gastoplasmic citernae are located beneath the thin organic layer.

At the veliger stage (Figure 15), proximal cells are evaginated and have spread over the body of the larva. This epithelium is now the larval mantle. The proximal cells adjacent to secreting cells arch upward and become the external cells of the outer fold of the mantle. These particular cells are termed proximal cells @. The intracellular space is still present at the apical region of the secreting cells. During the rest of the development, the external cells lengthen considerably (Figure 16). At the same time, the distal part of the secreting cells curves down to sink the secreted pellicle (Figure 17). This process corresponds to the formation of the periostracal groove. From this point onward, it is possible to distinguish two mantle folds; the outer fold is composed of external and secreting cells, while the microvilli cells are integrated into the inner fold.

The schematic representation of the chronology in shell elaboration during embryonic development of *P. maximus* is outlined in Figure 18.

DISCUSSION

In mollusks, shell elaboration results in morphogenetic events which include invagination and evagination of the shell field. It is generally accepted that for gastropods, scaphopods, and bivalves, the development of the shell field starts with the thickening of the median portion of the ectoderm in the dorsal region of the larva which later invaginates (Kniprath, 1981). In *P. maximus,* the time of appearance of the thickening of the dorsal epithelium has not been determined during embryogenesis. In this species, shell secretion begins when a reduced lumen is visible within the shell field. In *Mytilus galloprovincialis,* Kniprath (1979a, 1980) observed that shell pellicle formation takes place when the lumen of the shell field has totally disappeared. Eyster (1983) suggested that in *Aeolidia papillosa* initiation of shell secretion coincides with narrowing of the shell pore rather than with a closure of the lumen.

In *P. maximus,* primordial shell secretion is localized at the surface of the embryo and is elaborated by the cells forming the pore of the SFI, the secreting cells. In the gastropods *Lymnae stagnalis* and *Marisa cornuarietis* and in the bivalve *Mytilus galloprovincialis,* Kniprath (1979b) showed that the pellicle is secreted only by the non-invaginated cells. Similarly, Eyster (1983) indicated that in *Aeolidia papillosa* the shell pellicle is elaborated by the cells forming the pore of the SFI. Conversely, Eyster & Morse (1984) suggested that in the clam *Spisula solidissima,* the SFI is made up of two parts—a large outer part and a narrow inner one. According to these last authors, the shell pellicle is formed at the junction of these two parts. Therefore, it would seem that the pellicle of *Spisula solidissima* is formed in the SFI, which contradicts the results obtained for other species. Eyster & Morse (1984), however, suggested that the cells of the outer part of the invagination probably do not participate in shell formation. Elaboration of the shell pellicle by the cells forming the SFI pore has already been described in the early studies by Ziegler (1885) on *Cyclas* and Naef (1923, 1924) on *Lithoglyphus.* These authors gave an interesting functional significance to the shell gland or SFI. Indeed, they concluded that the marginal cells of the shell field join at the pore of the SFI and then secrete the shell pellicle, while the others cells of the epithelium are liberated from this function by the invagination. Thus, the invagination permits the formation of a shell pellicle without a central hole.

In *Aeolodia papillosa* Eyster (1983) defined three types of cells which constitute the shell field epithelium—growing edge cells, proximal cells, and microvilli cells. These three types of cells can also be differentiated in *P. max-*

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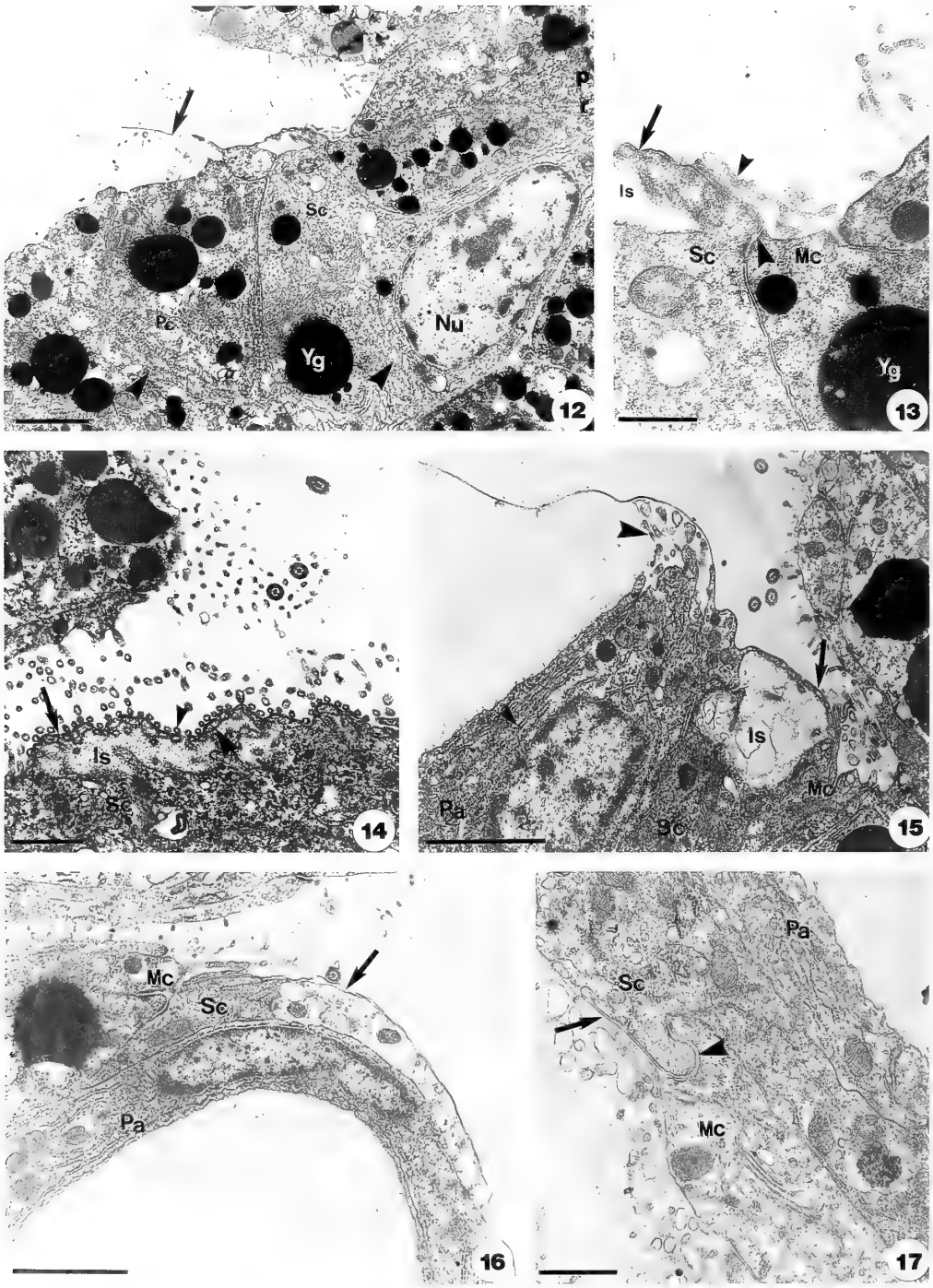
cytoplasmic extensions (↓) of the microvilli cells. TEM. Scale bar = 0.5 μm. Figure 9. Spreading of the shell pellicle (↓) at the surface of a 22 h embryo. Secreting cells (Sc) diverge, and the proximal cells (Pc) start to reach the surface; (Lu) SFI lumen; (Yg) yolk granules. TEM. Scale bar = 2 μm. Figure 10. The recently formed pellicle (arrow head) is covered by the microvilli of microvilli cells (↓), (Sc) secreting cells, (Yg) yolk granules. TEM. Scale bar = 0.5 μm.



Explanation of Figures 12 to 17

Figure 12. Longitudinal section through a 23 h trochophore; secreting cells (Sc) have an elongated basal nucleus (Nu) and a developed RER (arrow head); proximal cells (Pc) also possess a developed RER (↓) shell pellicle; (Yg) yolk granules. TEM. Scale bar = 2 μm. Figure 13. High magnification of apex of a secreting cell (Sc). A small part of the newly secreted pellicle (arrow head) arches downward between secreting and microvilli cells (Mc). Shell pellicle is covered by the cytoplasmic extensions (small arrow head) of the microvilli cells (Mc); (Is) Intracellular space; (Yg) Yolk granules. TEM. Scale bar = 0.5 μm. Figure 14. Apical region of a secreting cell (Sc) showing an intracellular space (Is); this space contains numerous minute electrodense granules. The shell pellicle (↓) is seen at the space apex covered by microvilli (small arrow head). Ergastoplasmic citernae (arrow head) lie under the pellicle. TEM. Scale bar = 1 μm. Figure 15. Young veliger of 30 h; proximal cells @ (Pa) adjacent to the

imus. Growing edge cells observed by Eyster (1983) correspond to secreting cells in *P. maximus*. As in *Aeolodia papillosa* (Eyster, 1983), the shell in *P. maximus* is formed at the apex of the secreting cells, at the distal edge of the cells with respect to the shell field invagination. An intracellular space is present at the apex of the secreting cells in this last species and the pellicle is formed at the surface of this space. This space contains many minute granules which may be free ribosomes. Just beneath the pellicle, RER citernae are observed, which are presumably involved in the synthesis of the organic pellicle. Presence of RER citernae beneath the pellicle and in the cytoplasm of the secreting cells indicates an important level of protein synthesis. This would tend to be in agreement with the results of Wilbur (1972) who noticed that the major shell component in mollusks is protein.

The microvilli originating from the microvilli cells which cover the newly formed pellicle probably protect this structure from the external environment. Protection of the recently elaborated shell pellicle has already been described during molluscan shell development. Indeed, in *Mytilus galloprovincialis,* Kniprath (1979a, 1980) observed that the first shell secretion is extracellular, the growing edge being situated between the intercellular space and the desmosomal zone where the newly formed pellicle is protected. In addition, the pellicle is covered by the glycocalyx and the microvilli originating from the cells adjacent to the pore cells. In *Aeolodia papillosa* Eyster (1983) also described microvilli cells protecting the recently secreted pellicle.

In bivalves, it is generally observed that the shell gland secretes the prodissoconch I, whereas the mantle elaborates the prodissoconch II. This is not true in *P. maximus* because the mantle is formed early during the development when the larva is secreting the prodissoconch I. Thus, at this time, the proximal cells @ adjacent to the secreting cells evaginate and form the outer cells of the outer fold of the mantle. Waller (1981) similarly suggested that in *Ostrea edulis* the transition of shell elaboration by the shell gland next to the mantle appears before the prodissoconch I is formed. In the literature, no detailed study is available on this transition. In *P. maximus,* the periostracal groove is developed when the larva are 45 hours old. At this time, the free margin of the mantle is composed of two folds as is observed in the majority of bivalve larva (Ansell, 1962; Cranfield, 1974; Cragg, 1976).

In the literature, shell calcification is generally associated with the formation of the prodissoconch I. In *P. maximus,* mineralization is not detected at the trochophore stage, but the D-veliger stage possesses a calcified shell. La Barbera (1974) described weakly birefringent bands in *Tridacna squamosa* at the posterio-dorsal area of late trochophores indicating the beginning of shell mineralization. Calcification has also been dectected at the trochophore stage in *Ostrea edulis* (Waller, 1981), *Spisula solidissima* (Eyster, 1986) and *Chlamys hastata* (Hodgson & Burke, 1988). In *P. maximus* prodissoconch I shell, calcification is situated near the hinge line and the shell margins. At this stage, La Barbera (1974) observed mineralization beginning at the shell hinge which then progresses on the ventral region of the shell to finally reach the center of the valves. Conversely, Waller (1981) observed that in *Ostrea edulis,* calcification is initiated in the center of the valves. The composition of the mineral part of the larval shell has been studied by Stenzel (1964) in *Crassostrea virginica* and *Mercenaria mercanaria.* He indicated that nearly all bivalves have an aragonic larval shell. Salaün (1994) suggested that in *P. maximus* the prodissoconch I consists of a single mineral layer composed of homogenous assemblage of vertical crystallites. Initiation of mineralization in *P. maximus* was not determined in this study; it would be of interest in future studies to determine the first appearence of mineral crystallites and their nature.

ACKNOWLEDGMENTS

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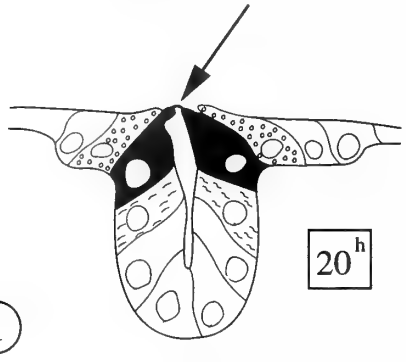
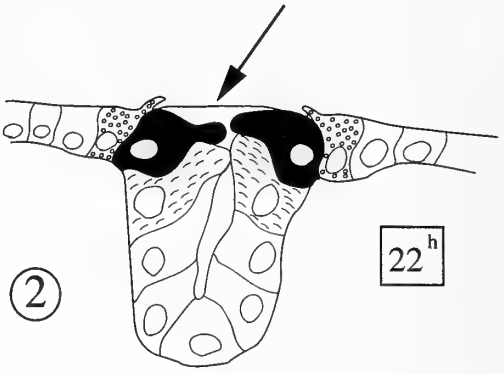
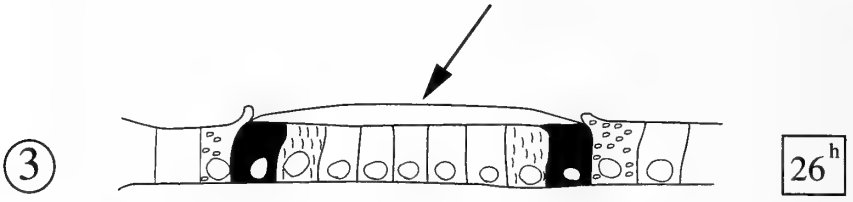
secreting cells (Sc) become the outer cells of the outer fold of the mantle. The outer cells bear microvilli (arrow head); its RER (small arrow head) is well developed. The shell pellicle (↓) is now secreted at the free margin of the mantle; (Is) intracellular space; (Mc) microvilli cells. TEM. Scale bar = 2 μm. Figure 16. Mantle free margin of a D-veliger of 45 h; on this section it is possible to distinguish a microvilli cell (Mc), a secreting cell (Sc), and an outer cell or a proximal cell @ (Pa) of the mantle. The latter has considerably elongated; (↓) shell pellicle; TEM. Scale bar = 2 μm. Figure 17. D-veliger of 45 h, the distal part of the secreting cells (Sc) curves down forming the periostracal groove. At this time, the new pellicle (arrow head) is protected in the periostracal groove; (Mc) microvilli cells; (Pa) proximal cells @; (↓) shell pellicle. TEM. Scale bar = 1 μm.



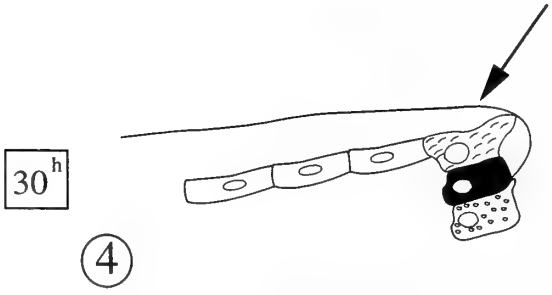
Beginning of shell pellicle elaboration, across the SFI aperture.



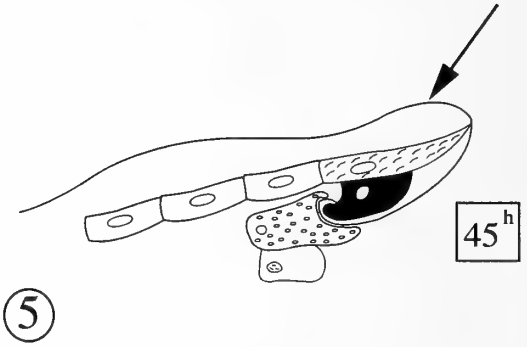
Spreading of shell pellicle ; proximal cells start to evaginate.



Evagination of SFI which becomes the larval mantle.



Proximal cells ⓐ arch upward and progressively elongate.



The mantle cells lengthen while secreting cells incurve downward leading to the formation of the periostracal groove.

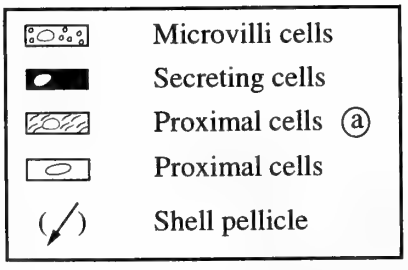


Figure 18

Chronological shell formation in *Pecten maximus* during embryogenesis.

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THE VELIGER

The Taxonomic Status and Redescription of *Polycera marplatensis* Franceschi, 1928 (Nudibranchia: Polyceratidae) from Argentina

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Abstract. The taxonomic status of *Polycera quadrilineata* var. *marplatensis* Franceschi, 1928, has been controversial since the original description. The species is redescribed here. It is consistently distinct in its internal and external morphology when compared with European specimens of *P. quadrilineata* (Müller, 1776). The internal anatomy is studied for the first time. A lectotype is designated for the species. The range of *P. marplatensis* is extended southward to the Magellanic Province.

INTRODUCTION

Franceschi (1928) described *Polycera quadrilineata* var. *marplatensis,* establishing the first record of the genus from Argentinian coasts. However, many of the features of his description could have been enough for it to be considered a new species instead of a variety of the European species *Polycera quadrilineata* (Müller, 1776). Odhner (1941) cited it as *Polycera marplatensis,* assigning it the rank of species; Pruvot-Fol (1954) synonymized it with *P. quadrilineata.* Risso Domínguez (1960) examined externally Franceschi's type material, and his own specimens collected in the same locality, and proposed *Galacera* as a new genus for this species.

In this study, we re-establish the taxonomic status of *Polycera marplatensis* as a valid species in the genus *Polycera* Cuvier, 1817; we redescribe the species using the type material and specimens collected in Patagonia.

SYSTEMATICS

Family Polyceratidae Alder & Hancock, 1845

Genus *Polycera* Cuvier, 1817

Polycera marplatensis Franceschi, 1928

(Figures 1–7)

Polycera quadrilineata var. *marplatensis* Franceschi, 1928: 577–586, figs. 1–7.

Polycera marplatensis Franceschi: Odhner, 1941:14–16; Marcus, 1958:50, fig. 4f, Castellanos, 1967:151.

Polycera quadrilineata marplatensis Franceschi: Carcelles, 1944:264.

Polycera quadrilineata (Müller, 1776) Pruvot-Fol, 1954: 315, fig. 126.

Galacera marplatensis (Franceschi) Risso Domínguez, 1960:56–62; Marcus & Marcus, 1967:197; Ríos; 1975: 170; Marcus, 1977:11; Ríos, 1994:210, fig. 1023, pl. 71.

Material examined: Type material deposited in the Museo Argentino de Ciencias Naturales, MACN: 17206. Intertidal, Mar del Plata (38°2′11″S, 57°31′37″W, Buenos Aires). 7 specimens, November 1927 collected by G. Franceschi. A holotype was not separated, so we here designate a lectotype MACN: 17206/1. Material from Patagonia (42°36′S, 64°16′W), 5 specimens collected by snorkeling (3–7 m depth) C. Muniain. 1 specimen (45 mm), 20 January 1992, 1 specimen (39 mm), 22 January 1992, 1 specimen (34 mm), 29 December 1993, 2 specimens (48 mm and 50 mm), 13 December 1995.

Diagnosis: Body limaciform, soft and smooth in appearance. White, with pigmented blotches and lines of yellow in the middle of the dorsum; laterally spotted with irregular yellow blotches, bearing small pallial tubercles. Tail showing a median yellow crest. Veil digitations usually seven, yellow. Large (30 to 50 mm length alive). Rhinophores bearing 12–21 lamellae. One pair of extrabranchial appendages. Gills nine, simply pinnate. Radular formula 4-5.2.0.2.4-5. Jaws exhibiting a winglike process. Penis bearing numerous hooked spines.

External features: The specimens collected from Mar

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Figure 1

Polycera marplatensis from Patagonia, living animal (50 mm).

del Plata (MACN:17206) are between 23 to 32 mm (total length alive, Franceschi's data), while the size of the Patagonian specimens is greater, 34 to 50 mm. The body shape is limaciform and elongate; coloration translucent white. The digestive tract is visible through the translucent tissue of the mantle. The appearance is soft and smooth (Figure 1). Two yellow lines are present on the border of the dorsum, from the veil to the extrabranchial processes. The middle of the dorsum shows yellow blotches and lines in random distribution. Uniformly spotted with irregular yellow blotches on the flanks, each blotch bearing a small central tubercle; in some animals these markings are imperceptible. The buccal region and dorsal veil anterior to the rhinophores bear an aggregation of orange-red blotches. A central raised but not knobbed, thick yellow crest stretches from the gills to the tail point. The foot is narrow, transversally grooved and with projecting margins. It shows a continuous line of yellow specks along the border.

The rhinophores bear between 12 to 21 lamellae, intense yellow in coloration, and are not retractile into their narrow sheaths. The base and the apex of the rhinophore are translucent. The first lamellae are occasionally spotted with black pigment. Seven or eight veil digitations are generally found, never fewer than six. The base is translucent, and the middle shows the identical yellow color as the blotches on the rest of the body, ending in lighter coloration.

The translucent white unipinnate gills have seven to nine branches. Usually seven are large, and the two posterior gills are smaller. The rachis have a yellow central streak, and are tipped with the same color, occasionally with black shadows below. The anus is posterior, between the smaller gill branches, and it has a yellow stippled border. The extrabranchial appendages are on either side of the gills, and they are longer than the big branches (Figure 2). An anomaly in two specimens was observed; one of them (39 mm) showed a bifurcated appendage, and the other specimen (45 mm) had four similar extrabranchial appendages on one side, which were smaller than the gills.

Anatomy: *Digestive tract.* A specimen 50 mm in length (Patagonia) was examined. The oral tube is elongate and large, while the buccal bulb is broad and rounded (length 4 mm, breadth 3 mm), without strong musculature, although it bears a short ventral muscle. In a radula sac lie the five newest teeth rows. The blood glands extensively cover the buccal bulb and the genital portion, connecting through the aorta with the heart. The salivary glands are

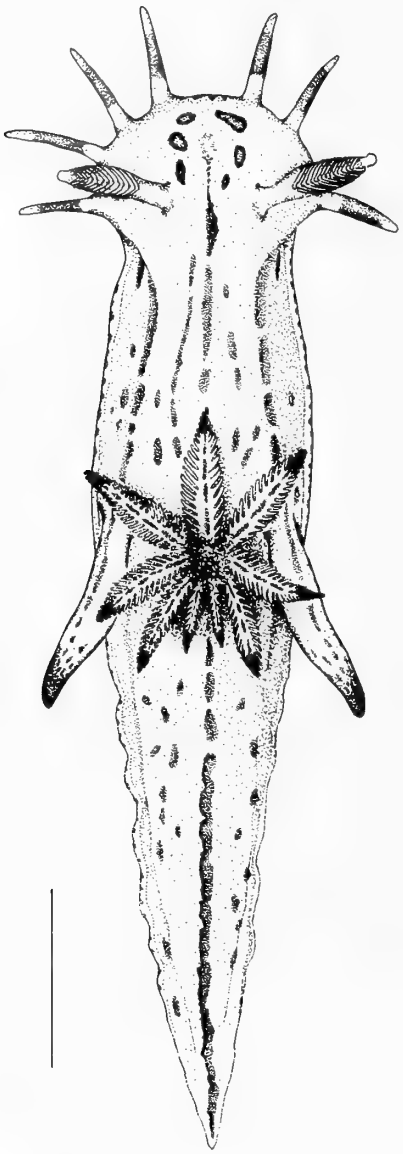

Figure 2

Dorsal view of a living animal showing the external features, scale bar = 8 mm.

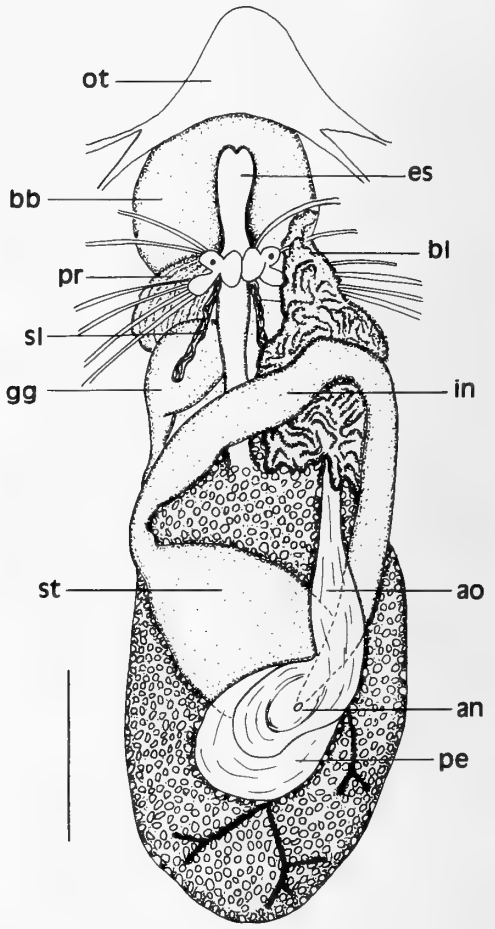

Figure 3

Anatomy (specimen from Patagonia, 50 mm). Dorsal view of the internal organs, scale bar = 5 mm. Key: **an,** anus; **ao,** aorta; **bb,** buccal bulb; **bl,** blood glands; **es,** esophagus; **gg,** gametolytic gland; **in,** intestine; **ot,** oral tube; **pe,** pericardium; **pr,** prostate; **sl,** salivary glands; **st,** stomach.

slender and flattened (5 mm). The long esophagus (14 mm) starts at the anterior portion of the buccal bulb and extends to the ample stomach which is enveloped by the digestive gland. From the stomach exits a large intestine (22 mm) which ends in the anus situated in the posterior portion of the gills (Figure 3).

Radula. The radular formula of a paratype 28 mm in length (MACN: 17206) is 14 × 4.2.0.2.4 (Figure 4A). The first lateral tooth is broad, with a curved cusp. It is at least half the size of the second lateral tooth (Figure 4B). The inner tooth bears a conspicuous, simple or bifid spur in the middle (Figure 4C). The outer, or second tooth lacks the spur, and the base is very broad. There are four marginal teeth; another rudimentary tooth may be present. They decrease in size toward the outside (Figure 4D). The jaw (2.1 mm in length) bears a winglike process, similar in shape to *P. quadrilineata* (Figure 5).

Reproductive system. The hermaphrodite ampulla is thin and enters the large female gland mass near the albumen gland (Figure 6A). The gametolytic gland is conspicuous and elongate, narrowing distally (8 mm total length). From it a single duct divides into the oviduct to the vagina, and a narrower insemination duct. The seminal receptacle is round, stalked, and arranged semi-serially on the insemination duct (Figure 6B). A very large prostate with folded walls continues into a deferens duct, which is slightly convoluted and expands into a thicker

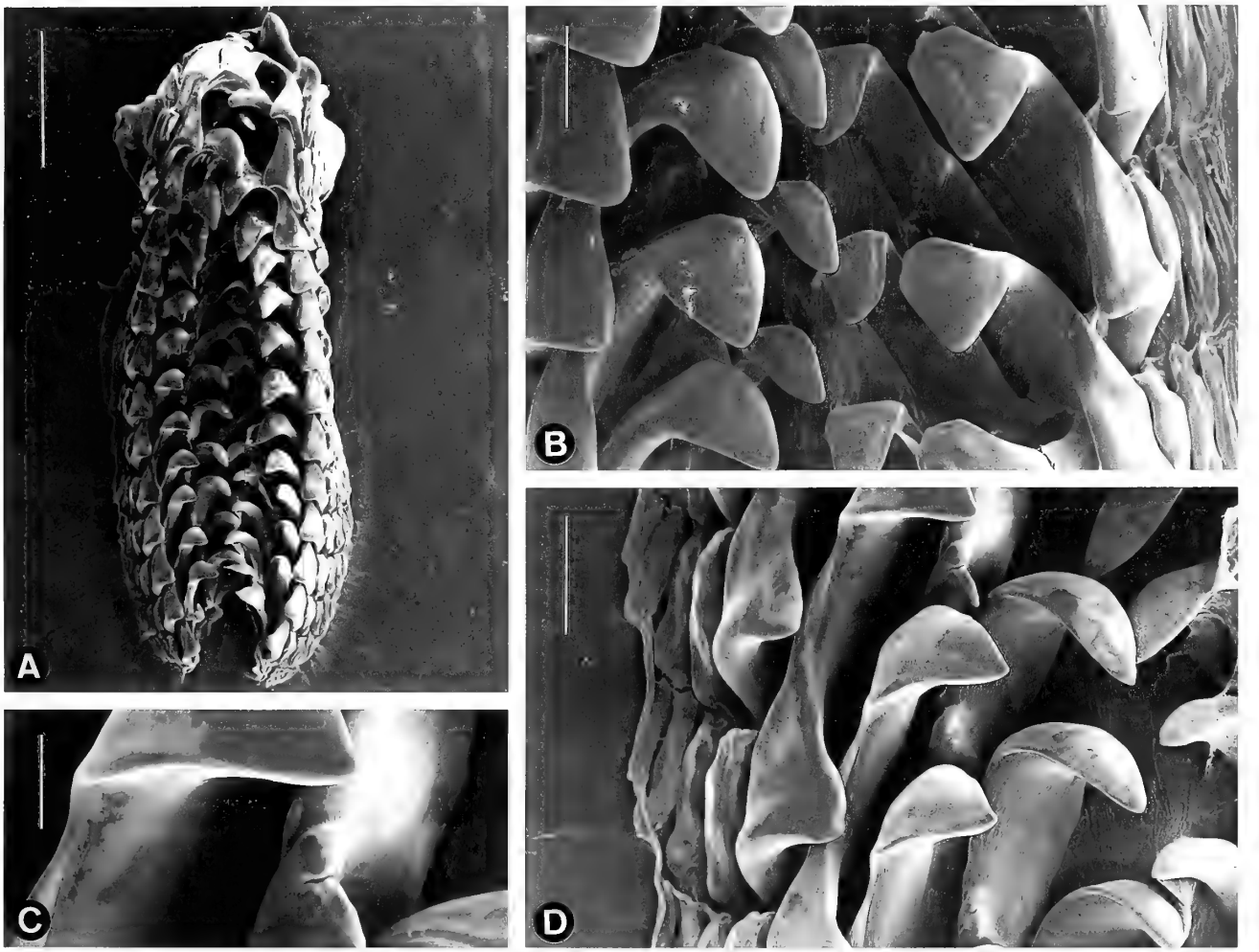

Figure 4

(A–D). Scanning Electron Micrographs of the radula of *Polycera marplatensis*. A. Entire radula, paratype (MACN: 17206, 28 mm), scale bar = 0.5 mm. B. First and second lateral teeth, scale bar = 100 μm. C. Detail of a bifid spur on the inner tooth, scale bar = 30 μm. D. Marginal teeth, scale bar = 100 μm.

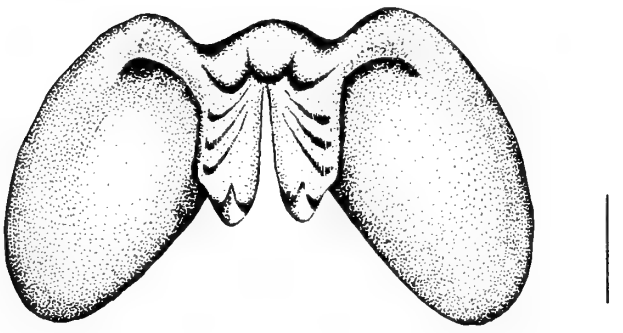

Figure 5

Jaw showing a winglike process (MACN: 17206, paratype: 28 mm), scale bar = 0.5 mm.

penial cirrus (1.2 mm breadth, 7 mm length). The cirrus bears numerous hooked spines throughout (Figure 7).

Distribution: West Atlantic distribution. The range of *P. marplatensis* extends from São Paulo (Brazil) southward to Patagonia, southern Argentina, an increase in its southern range from Mar del Plata (Buenos Aires). Specimens are abundant in the type locality Mar del Plata Port, where they live in the intertidal zone, on *Bugula,* an arborescent bryozoan on which they feed. From Patagonia the individuals were found submerged in at least 3 meters depth.

DISCUSSION

Franceschi (1928) assigned this taxon the systematic status of a variety of the European species *Polycera quad-*

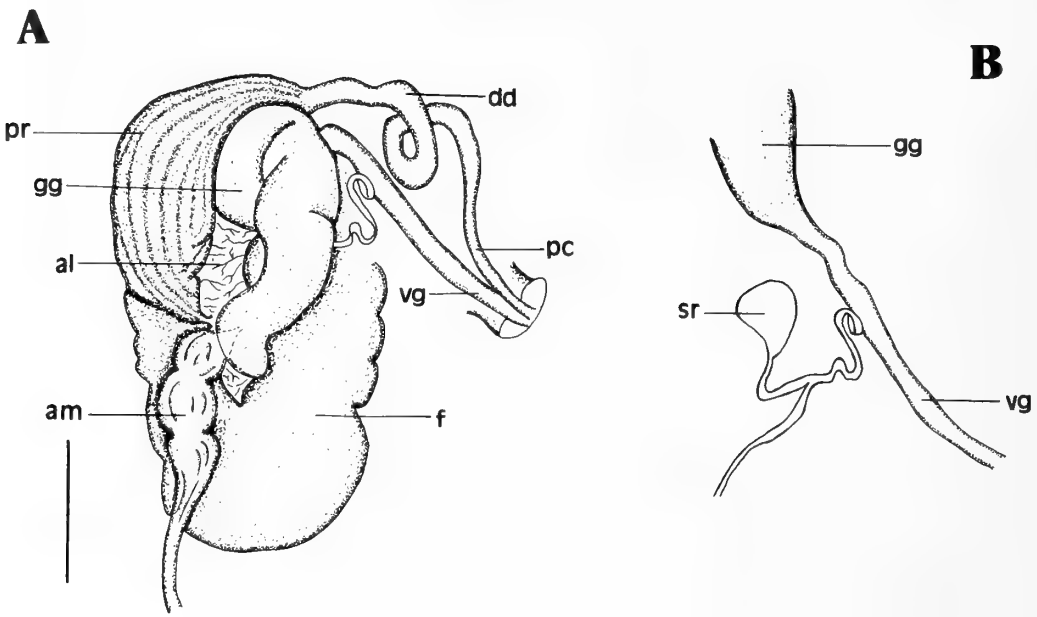

Figure 6

(A, B): Anatomy of the reproductive system (Patagonia, 50 mm), scale bar = 1.5 mm. Key: **al,** albumen gland; **am,** ampulla; **dd,** deferens duct; **f,** female gland; **gg,** gametolytic gland; **pc,** penial cirrus; **pr,** prostate; **vg,** vagina.

rilineata (Müller, 1776). His external description and discussion were good, and the features he noted have enough distinction to designate a new species. The larger size of the Argentinian specimens, the spotted and lined color pattern and the absence of black color on the body, the low elevation of pallial tubercules, and the smaller number of veil digitations suggest to us that this specimen should have the status of a new species. *Polycera quadrilineata* has four to six veil papillae, whereas *P. marplatensis* has seven to eight. In regards to the internal anatomy, the radulae and jaws differ only in size. Franceschi (1928) agreed with Bergh (1879) in considering that the fifth lateral tooth mentioned in *P. quadrilineata* by Meyer & Möbius (1872) was mistaken for a cuticle fold. We confirmed by our observations and those of Thompson & Brown (1984) that the radular formula can be 5.2.0.2.5 for specimens of *P. quadrilineata.* The presence of a vestibular gland found in *P. quadrilineata* (Schmekel & Portmann, 1982:389, fig. 11) is an important difference for separating it from *P. marplatensis,* which lacks this feature. The elongate gametolytic gland and the large prostate with folded walls seem to be a character common to the genus (Alder & Hancock, 1845–1855; Odhner, 1941; Schmekel & Portmann, 1982; García & Bobo, 1984). Odhner (1941:16) already mentioned the fact that Franceschi's *Polycera* could be a different species, but in his classification (based on Franceschi's description) commented incorrectly on the Argentinian species: "frontal digitations yellow, red in the middle" and "back surface with indistinct tubercles." That coloration in veil digitations, and distinguished tubercles on the surface have not been found among the type material and live specimens from Patagonia. Very small tubercles can be observed in the center of the lateral spots of only a few animals. Risso-Domínguez (1960) studied Franceschi's type material

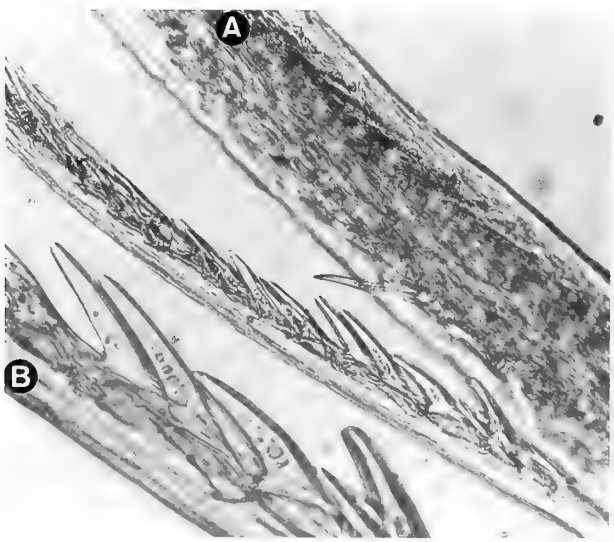

Figure 7

Optical Micrograph. A. Middle portion of the penial cirrus showing a row of hooked spines (100×). B. Detail of spines separated from the cirrus (200×).

externally, and proposed the genus *Galacera* based on the mistaken observation of rhinophores retractile into narrow sheaths, and without a tuberculate pallial margin. Marcus (1977) and Ríos (1975, 1994) mentioned that *Galacera marplatensis* occurs from the south of Brazil (São Paulo) to Argentina (Mar del Plata). The presence of spicules in the mantle is a common feature of the genus, having been mentioned by numerous authors. Calcareous spicules were not found in *P. marplatensis*; probably they had disappeared after fixation. Franceschi (1928) and Risso Domínguez (1960) did not mention spicules in their descriptions of the mantle from the type material. The most similar species to *Polycera marplatensis* is *P. quadrilineata,* which together with *P. capensis* Quoy & Gaimard, 1824, *P. atra* MacFarland, 1905, and *P. faeroensis* Lemche, 1929, are included in the white-yellow coloration pattern group. *Polycera marplatensis* only bears black blotches on the gills and at the bases of rhinophores, and does not show the black body pigmentation present occasionally in the rest of the species (except *P. faroensis*). In Odhner's (1941) classification, the group including *P. marplatensis* has the following characteristics: jaw with an upper winglike expansion, radula with inner lateral tooth at least half the outer one in size, and with a spur in its median length. *Polycera marplatensis* is easily separated from the rest of the Atlantic and Pacific species mentioned by Marcus & Marcus (1967), Ortea & Rolán (1989), and García & Bobo (1984).

The Magellanic Region includes some opisthobranchs common to the Pacific and Southern Atlantic coasts. Marcus (1959) described *Polycera priva* from Chile (44°30′S, 72°35′W) and M. Schrödl (personal communication) gave us data and a photograph of the living animals from the same region. *Polycera priva* has transparent coloration with white spots and lines, five gills, and three to five veil digitations. It lacks a wing expansion in the jaws (Marcus & Marcus, 1967). These characteristics clearly differentiate it from Atlantic species *P. marplatensis.*

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THE VELIGER

Synchronous Spawning and Reproductive Incompatibility of Two Bivalve Species: *Paphies subtriangulata* and *Paphies australis*

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Abstract. The bivalve species *Paphies subtriangulata* (Wood, 1828) and *Paphies australis* (Gmelin, 1791) are abundant in New Zealand waters and may occasionally occur in sympatry where their habitats overlap at harbor mouths. Spawning events involving simultaneous gamete release of both species were observed on several occasions in October 1993, suggesting the possibility of *in situ* hybridization. High *in situ* fertilization rates, ranging between 83.3% and 100% were obtained for *P. australis* during one of these October spawning events. Hybridization was examined *in vitro* through a series of cross-fertilization experiments and compared to intraspecific crosses and controls (oocytes of each species). The expected high fertilization rates for conspecific crosses were observed over all experiments, giving means of 90.8% SE ± 1.5% and 93% SE ± 0.6% for *P. subtriangulata* and *P. australis*, respectively. The interspecific crosses generally resulted in low levels of fertilization but, at high sperm concentrations, the *P. australis* sperm × *P. subtriangulata* egg cross showed a reasonably high level of fertilization (approx. 63%). At the same sperm concentration, the fertilization rate of crosses of *P. australis* egg × *P. subtriangulata* sperm did not differ significantly from sperm-free controls. We conclude that while the possibility of hybridization exists, the probability of significant levels of hybridization is minimal due to potential prezygotic reproductive incompatibility.

INTRODUCTION

In comparison with other mollusks, the reproductive biology of bivalves is relatively simple and unspecialized (Eversole, 1989). The sexes are usually separate, with gametes being released into the water column for external fertilization. This reproductive pattern is common among a large proportion of marine invertebrates (e.g., brachiopods, coelenterates, polychaetes, mollusks, and echinoderms). The success of this behavior is largely dependent on the existence of spawning synchrony within a species. The level of spawning synchrony in a localized population has been shown to affect fertilization success (Babcock & Mundy, 1992; Babcock et al., 1992). Aggregation of spawning individuals and sperm concentration can also affect fertilization rates (Pennington, 1985; Levitan et al., 1992). If large scale synchronous spawning events are rare within a population, their impact on reproductive output may be considerable (Babcock et al., 1994) because they may constitute the major reproductive events of the year for participating populations. However, external fertilization may create some problems in terms of the potential for hybridization and gamete wastage (Hodgson, 1988; Pearse et al., 1988).

Multispecific spawning events in which more than one species spawn at the same time are being reported with increasing frequency (McEuan, 1988; Pearse et al., 1988; Babcock et al., 1992; Van Veghel, 1993). Timing of spawning, habitat separation, and geographic isolation have been proposed as the main ecological factors inhibiting hybridization of closely related species within such groups (Strathmann, 1981; Uehara et al., 1990). In free-spawning invertebrates, gametic barriers to hybridization are particularly important as reproductive isolating mechanisms (Lessios & Cunningham, 1990; Palumbi & Metz, 1991). Barriers can occur at many points in the process including: induction of the "sperm acrosome reaction" by components of the egg surface, adhesion of sperm to the egg envelope, sperm penetration of the egg envelope, or fusion of sperm and egg cell membranes (Lee & Vacquier, 1992). Despite these possible isolating mechanisms, hybrids of a few taxa can be locally abundant at some locations (e.g., for the sea urchins *Echinus esculentus* and *Echinus acutus*, in which hybrids were found to compose 10–20% of the population [Hagström & Lönning, 1961]). Coustau et al. (1991) and Viard et al. (1994) also characterized the genetic structure of the *Mytilus edulis—M. galloprovincialis* hybrid zone on the coast of France, and found that the degree of hybridization was highly site-specific and dynamic, being influenced by ongoing mariculture activities. More stable genotypic structures have been determined for *Mytilus* hybrid zones in southwest England (Gardner & Skibinski, 1988).

Paphies subtriangulata (Wood, 1828) commonly inhabits the immediate sublittoral zone of exposed, open coast, fine-sand beaches throughout New Zealand (Redfearn, 1987), whereas *P. australis* (Gmelin, 1791) is found in more sheltered saline estuaries (Hooker, 1995a).

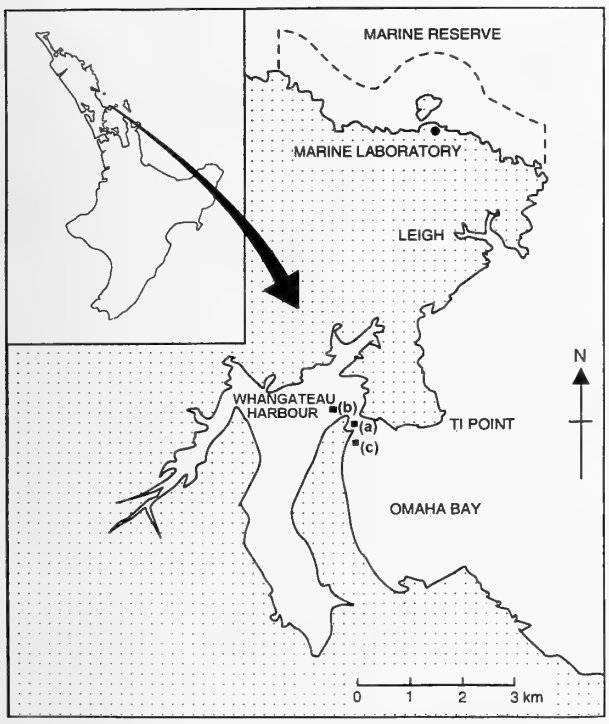

Figure 1

Little Omaha Bay and the adjacent Whangateau Estuary System, showing: a. the mixed *P. australis* and *P. subtriangulata* population, b. the main *P. australis* population, and c. the main *P. subtriangulata* population. The insert shows the location of these sites on the east coast of the North Island of New Zealand.

In Omaha Bay, northeastern New Zealand, populations of *P. subtriangulata* (tuatua) and *P. australis* (pipi) were found to coexist within the same bed at a transition site between the harbor mouth and the adjacent exposed sandy beaches (Figure 1a). This area constituted approximately 1% of the area of combined *P. australis* and *P. subtriangulata* habitat. While this was not a frequent event, such overlapping may occur at other harbor mouths around New Zealand. The overlapping distribution pattern, combined with overlapping spawning periods (for *P. australis* see Hooker & Creese, 1995a, b; for *P. subtriangulata* see Grant & Creese, 1995), resulted in *in situ* synchronous spawning of pipi and tuatua on several occasions in October 1993 (Grant & Creese, 1995). This presented the opportunity to collect data on natural fertilization rates of these bivalve species. The possibility that natural hybridization might also be occurring during such synchronous (within seconds) spawning events suggested that the *P. subtriangulata–P. australis* mating systems should be examined in order to ask whether the two species are isolated by pre-zygotic reproductive barriers, or whether they represent distinct species able to interbreed, but maintained by temporal or spatial barriers to hybridization.

MATERIALS AND METHODS

Hybridization Experiments

Collection of specimens and gametes: The initial hybridization experiment (November 1993) followed observations of *P. australis* and *P. subtriangulata* spawning synchronously on a number of occasions during October 1993 (Grant & Creese, 1995). Adult *P. subtriangulata* and *P. australis* (>50 mm shell length) were collected from the mixed population in Omaha Bay, northeastern New Zealand (Figure 1a) on 4 November 1993 and 26 August 1994 (experiments 1 and 2), when adults of both *P. subtriangulata* and *P. australis* were known to be in the ripe phase (Grant & Creese, 1995; Hooker & Creese, 1995a, b). The third experiment (27 July 1995) involved *P. subtriangulata* collected from Omaha Bay (Figure 1c) and *P. australis* collected from the nearby Whangateau Harbour (Figure 1b).

For each of the three experiments, a sample of approximately 40 *P. australis* and 40 *P. subtriangulata* were haphazardly collected by SCUBA (in water depths of 1–3 meters below MLW) from the Omaha and Whangateau study sites and transported back to the Leigh Marine Laboratory. Specimens were stored out of water until the experiment was initiated (for a period of < 1 hour) to prevent any inadvertent gamete release. All instruments coming in contact with specimens were cleaned and rinsed with freshwater between handling and opening of separate individuals. Specimens were opened, and a gonad biopsy undertaken using a light microscope to determine the sex of each individual. Eggs and sperm were then stripped from the gonad region by making incisions into the visceral mass, and teasing out the ripe gametes.

The subsequent sperm solutions were examined microscopically to evaluate the motility of spermatozoa, allowing us to discard any unripe individuals. The resulting male and female gametes were pooled for each species (approximately eight individuals of each sex were used) and suspended in 500 ml of filtered seawater (1 μm) at ambient seawater temperature.

For each experiment, interspecific crosses (*P. subtriangulata* sperm × *P. australis* egg and *P. subtriangulata* egg × *P. australis* sperm), as well as intraspecific crosses (*P. australis* egg × sperm and *P. subtriangulata* egg × sperm) were carried out. This study simultaneously included controls (oocytes in 1 μm filtered seawater) for spontaneous parthenogenetic development. Four replicates were used for each treatment and control in the first and second experiments, and three replicates of each treatment and control within each sperm dilution for the third experiment.

Experiment 1: This initial experiment served as a pilot

study; thus accurate sperm concentrations were not used. Automatic micro-pipettes were used to measure 4 ml of egg suspension, which was subsequently mixed with one drop of sperm solution, within half an hour of gamete stripping. Fertilization success was assessed by light microscopy (×200) 2–3 hr post gamete mixing when numbers of fertilized and unfertilized eggs were recorded for each replicate within each cross. Fertilization was considered successful when cleavage of the egg (two or four cell stage) was clearly visible. For overall comparison of fertilization success among the various crosses, results from each replicate were combined to obtain the mean percent fertilization (±SE) for each cross.

Experiment 2: Automatic micro-pipettes were used to measure 2.5 ml replicates of egg suspension, which were subsequently mixed with 0.01 ml of sperm solution. Fertilization success was assessed as in Experiment 1.

Experiment 3: This experiment tested a range of sperm concentrations. Freshly stripped sperm (placed in approximately 500 ml of 1 μm filtered seawater) were immediately diluted in a ten-fold dilution series. Sperm concentrations were assessed by haemocytometer counts of sperm in the initial suspension. Three ml of filtered seawater (1 μm), 4 ml of egg suspension (*P. subtriangulata* - 33 eggs/ml and *P. australis* - 48 eggs/ml) and 1 ml of sperm suspension was added to three replicate vials. This procedure was replicated for the following three sperm dilutions: 1:10 dilution: *P. australis* sperm $9.92 \pm 1.8 \times 10^5$ ml, *P. subtriangulata* sperm $1.05 \pm 1.2 \times 10^6$ ml; 1:100 dilution: *P. australis* sperm $9.92 \pm 1.8 \times 10^4$ ml, *P. subtriangulata* sperm $1.05 \pm 1.2 \times 10^5$ ml; 1:1000 dilution: *P. australis* sperm $9.92 \pm 1.8 \times 10^3$ ml, *P. subtriangulata* sperm $1.05 \pm 1.2 \times 10^4$ ml. Gametes were mixed within 1 hour of stripping. Fertilization success was assessed by light microscopy (×200) 2–3 hr post gamete mixing when numbers of dividing (assumed to be successfully fertilized), and non-dividing eggs, and those still containing the germinal vesicle were recorded for each replicate within each cross. Samples were maintained to allow any further development to occur and were reclassified as mobile larvae, non-mobile larvae, or non-viable after 24 hrs.

Natural Fertilization Rates

During the observed synchronous spawning of *P. subtriangulata* and *P. australis* on 21 October 1993 (Grant & Creese, 1995), egg samples were collected *in situ* from spawning female pipi to enable the enumeration of natural fertilization rates. Samples were collected from female individuals spawning in positions that were either "aggregated" (males releasing sperm positioned within 1 m, usually < 15 cm, n = 4) or "isolated" (no males seen releasing sperm within a 1 m radius, n = 3). Egg samples were collected using a submersible plankton pump, which allowed collection and storage of separate samples during the same dive (see Mundy et al., 1994 for a detailed description of the sampling procedure and pump design). On return to the laboratory, samples were preserved in 10% seawater formalin to allow examination and analysis of fertilization success. A subsample of fixed eggs was subsequently scored as fertilized or unfertilized. Fertilization success was measured by light microscopy as the proportion of eggs which had undergone cell division.

RESULTS

Hybridization Experiments

Experiment 1: Mean fertilization rates in the within-species crosses were high; 95.8% (SE ± 1.9%) and 97.5% (SE ± 0.3%) for *P. subtriangulata* and *P. australis*, respectively (Figure 2a). The controls showed low mean fertilization levels; *P. subtriangulata* eggs − 4.5% (SE ± 1.6%) and *P. australis* eggs − 5.9% (SE ± 1.5%). Interspecific crosses between *P. subtriangulata* and *P. australis* resulted in fertilization rates lower than those in the controls in the *P. subtriangulata* egg × *P. australis* sperm treatment (approx. 2%, Figure 2a), while the reciprocal cross exhibited zero fertilization.

Experiment 2: Mean fertilization rates in the intraspecific crosses were again high: 94% (SE ± 3.5%) and 99.9% (SE ± 0.1%) for *P. subtriangulata* and *P. australis*, respectively (Figure 2b). Both interspecific crosses resulted in low levels of fertilization; *P. subtriangulata* egg × *P. australis* sperm; 9.4% (SE ± 1.2%), *P. australis* egg × *P. subtriangulata* sperm; 5.3% (SE ± 1%) (Figure 2b). The controls showed low levels of fertilization; *P. subtriangulata* eggs a mean of 8.7% (SE ± 0.8%) and *P. australis* eggs a mean of 6.2% (SE ± 0.5%). The two hybrid crosses were not significantly different from each other, or from either of the control treatments (Student-Newman-Keuls Method, $P < 0.05$).

Experiment 3: The mean fertilization rates in the intraspecific crosses were consistently high; 83–93% and 82–92% for *P. australis* and *P. subtriangulata*, respectively. Asymmetrical hybridization was apparent in the interspecific crosses with *P. subtriangulata* egg × *P. australis* sperm having higher rates of fertilization than the reciprocal cross. However, sperm concentration had a marked effect on the level of asymmetry (Figure 3a, b, c). The *P. australis* sperm × *P. subtriangulata* egg cross displayed high levels of fertilization at high sperm concentration, but decreasing fertilization success at lower sperm concentrations (i.e., 62.7 to 31.2 to 6.7%). A one-way ANOVA ($df = 17,36$; $P < 0.0001$, data were square-root arcsin transformed to fit the normality assumption) was performed on all possible cross and control interactions, for each dilution, and showed that the differences in the mean values among the treatments was greater than that expected by chance. *A posteriori* pairwise multiple com-

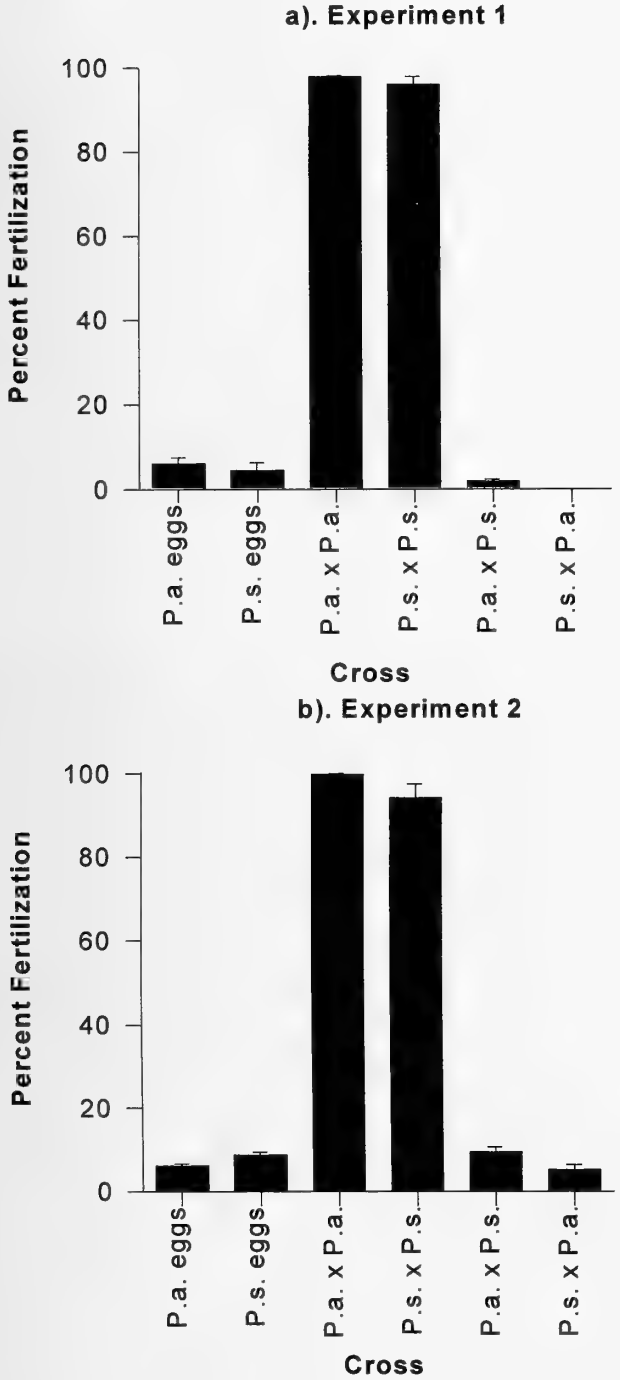

Figure 2

a. Experiment 1. Mean fertilization rates (%) for *P. australis*/*P. subtriangulata* treatments and controls. Values are means of four replicates ± SE. For each cross, the male is indicated first. P.a.: *Paphies australis*; P.s.: *Paphies subtriangulata*. Controls (shown in the first two columns) consist of eggs from each species. b. Experiment 2. Data are presented in the same format as in a.

parison (Student-Newman-Keuls Method, $P < 0.05$) tests showed that: (1) At the 1:10 sperm concentration, the *P. subtriangulata* intraspecific cross had significantly higher fertilization than the *P. australis* intraspecific cross, whereas at the other dilutions there was no significant difference; (2) the *P. australis* male × *P. subtriangulata* female had significantly higher fertilization at the 1:10 sperm dilution than its reciprocal cross, but at the 1:1000 dilution, there was no significant difference between the two hybrid crosses; (3) the *P. australis* male × *P. subtriangulata* female cross was also significantly greater than both controls at all dilutions; (4) the *P. subtriangulata* sperm × *P. australis* egg cross was not significantly different from either of the controls at any dilution.

After approximately 24 hours of development, large numbers of the fertilized eggs had not developed into trochophores (Figure 4), indicating that development was constrained at this stage. This was not unexpected in stripped gametes. While bivalve oocytes stripped from gonads may be fertilized, it is commonly found that development does not proceed beyond early stages, presumably due to the fact that gametes not shed in the process of natural spawning are insufficiently mature to develop normally.

The highest proportions of mobile larvae were, as expected, found in the intraspecific crosses. The only other treatment to contain mobile larvae (assumed to be healthy) was the *P. australis* male × *P. subtriangulata* female cross. For this cross, the proportion of mobile larvae decreased with increasing sperm dilution, from approximately 26% (dilution 1:10) to 2% (dilution 1:1000).

Natural Fertilization Rates

High levels of fertilization were obtained for naturally fertilized *P. australis* eggs collected *in situ* from Omaha Bay in October 1993. These ranged from 100% (n = 4) for spawning females within "aggregates" to 83.3%, SE ± 15.3% (n = 3) for "isolated" females.

DISCUSSION

High rates of fertilization were recorded for *P. australis* during *in situ* spawning observations that also coincided with *P. subtriangulata* spawning. These are the first measurements of natural fertilization rates from a free-spawning bivalve mollusk. Even eggs from females which were relatively isolated from surrounding males (i.e., no males releasing sperm within a 1 m radius) achieved high levels of fertilization. This indicates that, even in small organisms living at relatively low densities, spawning can be highly successful. This may be true even when a low proportion of the population are synchronously spawning. By comparing this site to a similar site farther along Omaha Beach (Figure 1c), with densities of tuatua measured at 8/m^2 (Grant, 1994), we estimate the density of

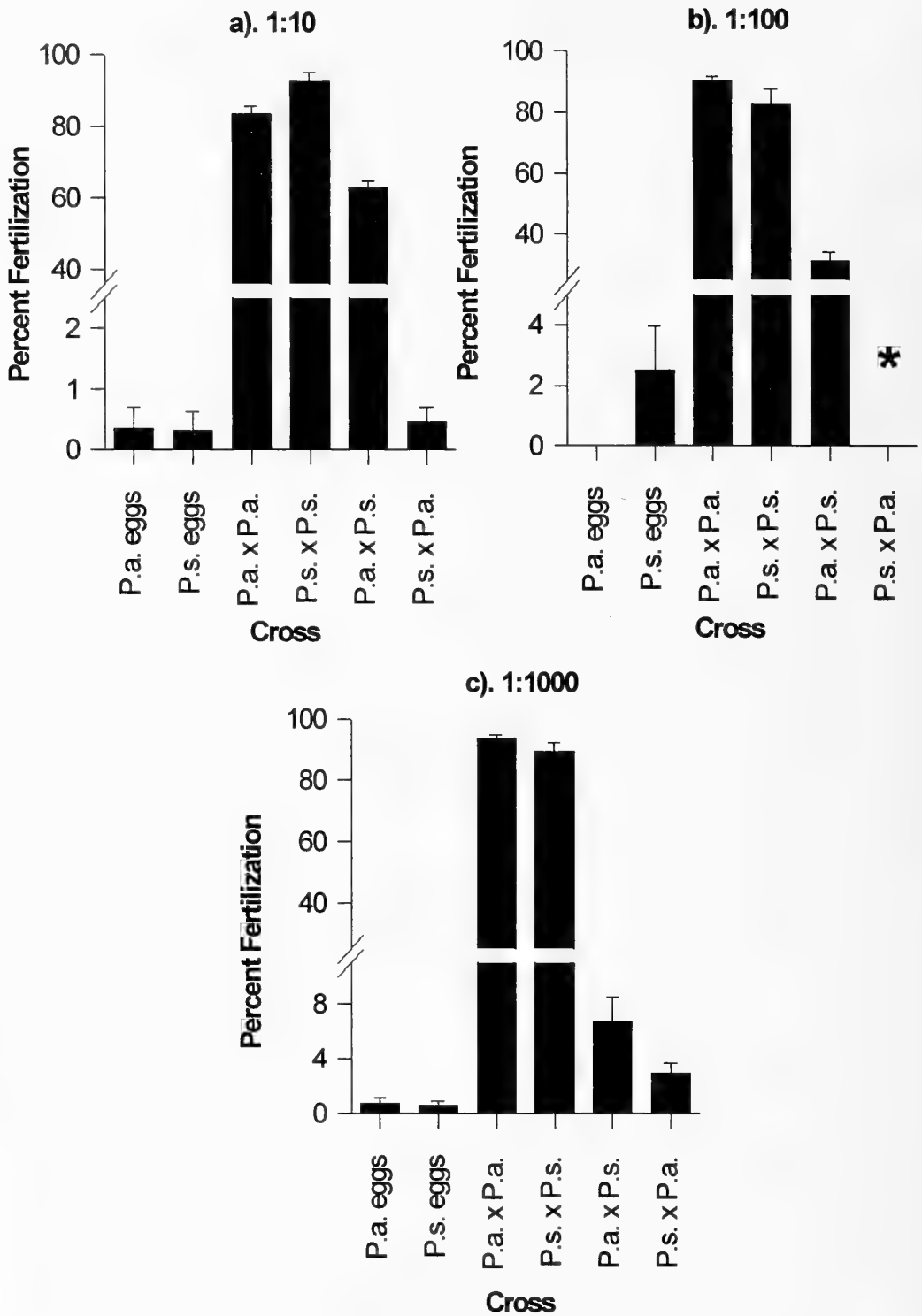

Figure 3

Mean fertilization rates (%) for *P. australis*/*P. subtriangulata* treatments and controls at 3 sperm dilution rates (a = 1:10, b = 1; 100 and c = 1:1000), experiment 3. Values are means of three replicates ± SE. Data presented in the same format as Figure 2. * = No data.

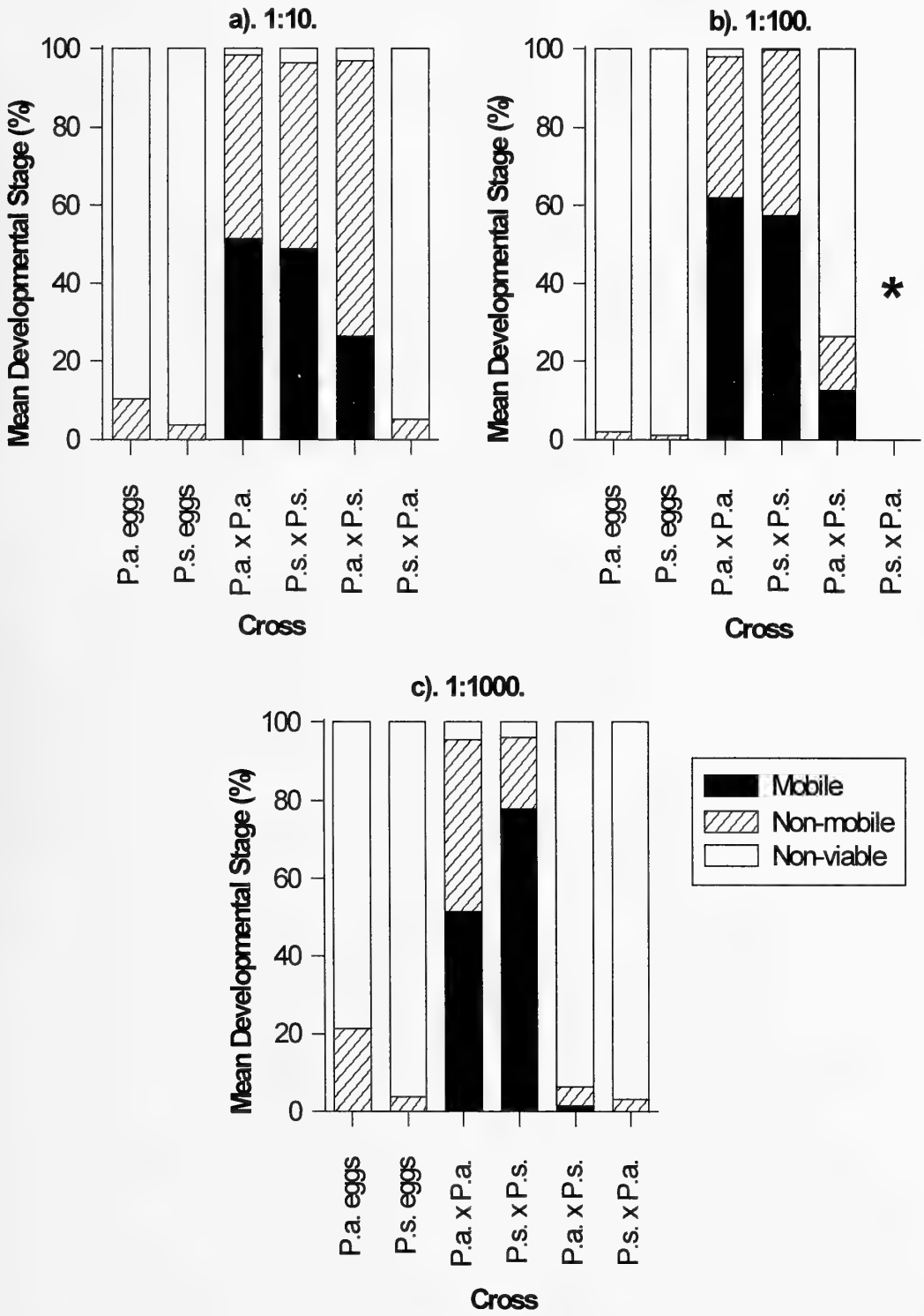

Figure 4

Mean Developmental Stage after 24 hr for *P. australis/P. subtriangulata.* Data are the % of mobile, non-mobile and non-viable larvae at 3 sperm dilution rates (a = 1:10, b = 1:100 and c = 1:1000). Values are means of three replicates from Experiment 3. Data presented in the same format as Figure 2. * No data.

tuatua at the mixed population site to be 1/m^2, with only 40% of this population spawning.

These high natural fertilization rates are consistent with those of previous field studies of naturally spawning marine invertebrates (e.g., Babcock et al., 1992; Oliver & Babcock, 1992), as well as with laboratory-based modeling studies of fertilization in *Cerastoderma edule*, another free-spawning bivalve (André & Lindegarth, 1995). André & Lindegarth (1995) estimated that at a density of 1 cockle/m^2, sperm concentrations should be in the order of 10^2–10^3 μl^{-1} in patches of animals with dimensions of 10–100 m (average flow speed of 0.01 m s^{-1}, water depth = 0.1 m). Their results indicate that at these sperm concentrations fertilization rates ranging from as low as 10% to as high as 80% might be expected. Spermatozoan longevity may also play a key role in fertilization success. Andre & Lindegarth (1995) found that fertilization was impossible after 4–8 hr for *Cerastoderma edule*, as viability of both eggs and sperm decreased with age. This could be particularly important for species in which population density is low and/or there are no aggregative or pseudocopulatory behaviors at the time of spawning (Benzie & Dixon, 1994). *P. australis* often displayed a pre-spawning behavior of moving to a position halfway out of the sediment. This behavior was not displayed by *P. subtriangulata* and may affect the distribution of sperm between the two species. Although natural spawning was observed for *P. subtriangulata* as well (Grant & Creese, 1995), no data on natural fertilization rates were obtained.

In mollusks, as well as in echinoderms and corals, it appears that although fertilization success may be variable, high fertilization rates can be achieved, given the degree of spawning synchrony that we observed. This is not to downplay the potential for reproductive failure due to low fertilization rates. Spawning observations made in this system were typically on very calm days with little, if any, wave action. Wave action could highly modify fertilization success at this site; if turbulent mixing was high, then sperm and ova could be rapidly diluted beyond the point at which fertilization would be successful (Denny & Shibata, 1989). Nevertheless, the usual result of spawning, even for less aggregated individuals, may well be higher fertilization rates for this bivalve than those suggested by Pennington (1985) for echinoderms.

Experiments conducted in the laboratory produced fertilization rates for within-species crosses that were similar to those for aggregated *P. australis* in natural spawning situations. In Experiment 2, the *P. australis* intraspecific cross had significantly higher fertilization than the *P. subtriangulata* intraspecific cross; however, we feel this is not ecologically significant and may simply be related to the fact that *P. subtriangulata* gametes are more difficult to strip in a laboratory situation. Positive results were recorded in at least four out of six hybrid crosses in Experiment 3. In most cases, low levels of fertilization were observed (i.e., not significantly different from the controls), but sperm dilutions of 1:10 and 1:100 (*P. australis* sperm × *P. subtriangulata* egg) gave high levels of fertilization (approx. 63% and 31%, Figure 3a, b). Hybrid fertilization was also followed by some successful development through to the trochophore stage (Figure 4a, b).

Although fertilization was successful, few embryos developed to the veliger stage and all died shortly afterward, indicating that larval viability at 24 hr was not a good indicator of long-term survival of hybrids. Gaffney & Allen (1993), in summarizing hybridization experiments for *Crassostrea* spp., noted that even interspecific crosses which readily yield active larvae often fail to produce long-term viable hybrids. "Control" eggs never developed beyond the cleavage stage (Figure 4a, b, c), which may suggest that cleavage in control crosses is promoted by the mechanics of stripping and causes abortive oocyte activation. For many species it has been found that eggs obtained by stripping result in low proportions that develop normally (Chanley, 1975; Loosanoff & Davis, 1963). Hooker (in press) found that attempts at stripping eggs for fertilization experiments from *P. australis* always resulted in very low numbers of healthy larvae at any time of the year.

There is clearly potential for gametes of each species to encounter one another in nature, as evidenced by simultaneous spawning of these species on three occasions in October 1993 (Grant & Creese, 1995). The two species at this site both appeared to spawn in response to temperature change on the outgoing afternoon high tide (Grant & Creese, 1995). With an apparently common cue for spawning, as well as the possibility of overlapping spatial distribution and similar gametogenic cycles, occasional simultaneous, heterospecific spawnings of *P. australis* and *P. subtriangulata* appear to be inevitable. Other New Zealand species of the genus *Paphies* (*P. donacina*, the deep water tuatua and *P. ventricosa*, the toheroa) also have geographic and habitat distributions, as well as reproductive cycles, that may overlap with *P. australis* and *P. subtriangulata* to varying degrees. For example, *P. ventricosa* and *P. subtriangulata* have on occasion been found in the same bed (Redfearn, 1974; Stace, 1991). Conchological evidence of a variety of forms of surviving hybrids in natural populations of *Paphies* species do exist (G. Stace, personal communication, Auckland Museum).

Hybrid sterility and inviability can be important factors in reproductive isolation, but in the *P. australis-P. subtriangulata* system it would seem that even though asymmetric hybridization may take place, pre-zygotic barriers are probably most important in maintaining barriers to gene flow in present populations. We speculate that the ability to discriminate between conspecific and heterospecific gametes in these species may provide some selective benefit to the species by preventing gamete wastage resulting from the formation of inviable hybrid zygotes, but the viability, or otherwise, of hybrid trocho-

phores or later stage larvae has yet to be established. This is especially true where synchronous spawning occurs. If there are post-gametic developmental barriers to hybridization, as may be found to be the case for *P. australis* × *P. subtriangulata* hybrids, synchronous spawning may be a source of gamete wastage.

In situ measurements of fertilization and laboratory experiments indicate that sperm concentrations in the field, which produce concentrations of > 90%, are likely to be of the same order as those used in the laboratory experiments that produced mobile hybrid larvae. However, based on a conservative comparison, fertilization rates in the field suggest sperm concentrations no higher than $\sim 1 \times 10^4$ sperm/ml, (equivalent to 1:1000 dilution). Consequently, the potential for hybrid formation is likely to be low, principally mediated by gamete level interactions dependent on sperm density. This factor plus the asymmetrical nature of the gamete interactions and the relatively small degree of habitat overlap between *P. australis* and *P. subtriangulata* means that numbers of hybrids in the population are likely to be low. Investigation of the potential for hybridization among these species might provide useful insights into the mechanisms that maintain their specific status (especially the genetic separation of the two species of tuatua as defined by Richardson et al., 1982), as well as possible evolutionary mechanisms in this group (cf. Lee & Vacquier, 1992).

Interspecific and intraspecific crosses were not reared through to settlement, but there is clearly a need to establish the long-term developmental potential of these hybrid larvae. Further laboratory and field studies should also be conducted to examine sperm competition outcomes in mixed species sperm suspension. Ideally this would be done using genetic markers that might also allow identification of natural hybrids in the field.

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Additions to the Late Paleocene Molluscan Fauna from the Santa Monica Mountains, Los Angeles County, Southern California

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Abstract. Several previously unreported shallow-marine, warm-water gastropods and bivalves from the upper part of the Santa Susana Formation, east–central Santa Monica Mountains, Los Angeles County, southern California, are described and discussed. The gastropods are *Diodora* sp. nov.? (Fissurellidae) and *Terebralia* ***susana*** sp. nov. (Potamididae). The bivalves are *Solena* (*Eosolen*) *stantoni* (Weaver, 1905) (Solenidae), *Martesia* sp. (Pholadidae), and *Nototeredo*(?) sp. (Teredinidae). These mollusks are of late Paleocene (Thanetian Stage) age. For the Pacific Coast of North America, the specimens of *Diodora* and *Martesia* represent the earliest records, the specimens of *Terebralia* the first confirmed record, and the specimens of *Nototeredo*(?) the first record. The specimens of *Solena* (*Eosolen*) *stantoni* are the best preserved and largest of this species.

INTRODUCTION

The late Paleocene was a time of a large influx of migrant shallow-marine mollusks into the Pacific Coast region of North America via circum-global tropical circulation, and this influx continued on into the early Eocene (Zinsmeister, 1983a; Squires, 1988). Upper Paleocene marine rocks are uncommon on the Pacific Coast of North America but are well represented in the Palisades Highlands area in the east-central Santa Monica Mountains, southern California (Figure 1). Although natural outcrops are scarce due to extensive vegetative cover, shallow-marine mollusks have been found locally, particularly in new exposures temporarily uncovered by bulldozer activity during the construction of homesites. Most of the specimens of rare and previously unreported mollusks that are the focus of this paper were collected during the past 15 years by J. M. Alderson and W. L. Rader, who donated them to local museums. These mollusks are the gastropods *Diodora* sp. nov.? and *Terebralia* ***susana*** sp. nov., and the bivalves *Solena* (*Eosolen*) *stantoni* (Weaver, 1905), *Martesia* sp., and *Nototeredo*(?) sp.

The following institutional acronyms are used: CSUN, California State University, Department of Geological Sciences, Northridge; LACMIP, Natural History Museum of Los Angeles County, Section of Invertebrate Paleontology, Los Angeles; and UWBM, University of Washington, Thomas Burke Memorial Museum, Seattle.

STRATIGRAPHY

The mollusks discussed in this report were collected from the area east of Santa Ynez Canyon, in the tributaries of Quarry Canyon, Trailer Canyon, Pulga Canyon, and other unnamed tributaries (Figure 1). All the localities plot within the upper part of the Santa Susana Formation as mapped by Dibblee (1992). Colburn et al. (1988) and Colburn (1996) assigned the Paleocene rocks here to the Santa Susana Formation, in its broad sense, although other recent workers (e.g., Saul, 1983; Strathearn et al., 1988) referred to them as the Coal Canyon Formation of Yerkes & Campbell (1979).

The upper part of the Santa Susana Formation in the Santa Ynez Canyon area is a marine unit consisting mostly of olive to gray-green, fine-grained sandstone and siltstone, which are bluish gray when unweathered. Megafossils are either in thin lenses or scattered throughout the beds. Within the upper part of the formation there are outcrops of coralline-algal limestone, which are white and resistant. These might represent a single stratigraphic unit that is present in minor fault blocks and/or landslide blocks, or they might represent multiple units of similar lithology. Previous geologic studies in the area have failed to clarify the stratigraphic relationships. Colburn et al. (1988), in a study of the Santa Susana Formation in the Santa Monica Mountains, considered the algal limestone to make up a single 10 m-thick marker bed in the formation. Strathearn et al. (1988) reported several lenses of algal limestone. Mack (1993) reported that the algal limestones (10 to 30 m thick) apparently represent several stratigraphic levels. Strathearn et al. (1988) and Mack (1993), however, grouped all of the algal limestones into a single stratigraphic unit in their generalized stratigraphic columns.

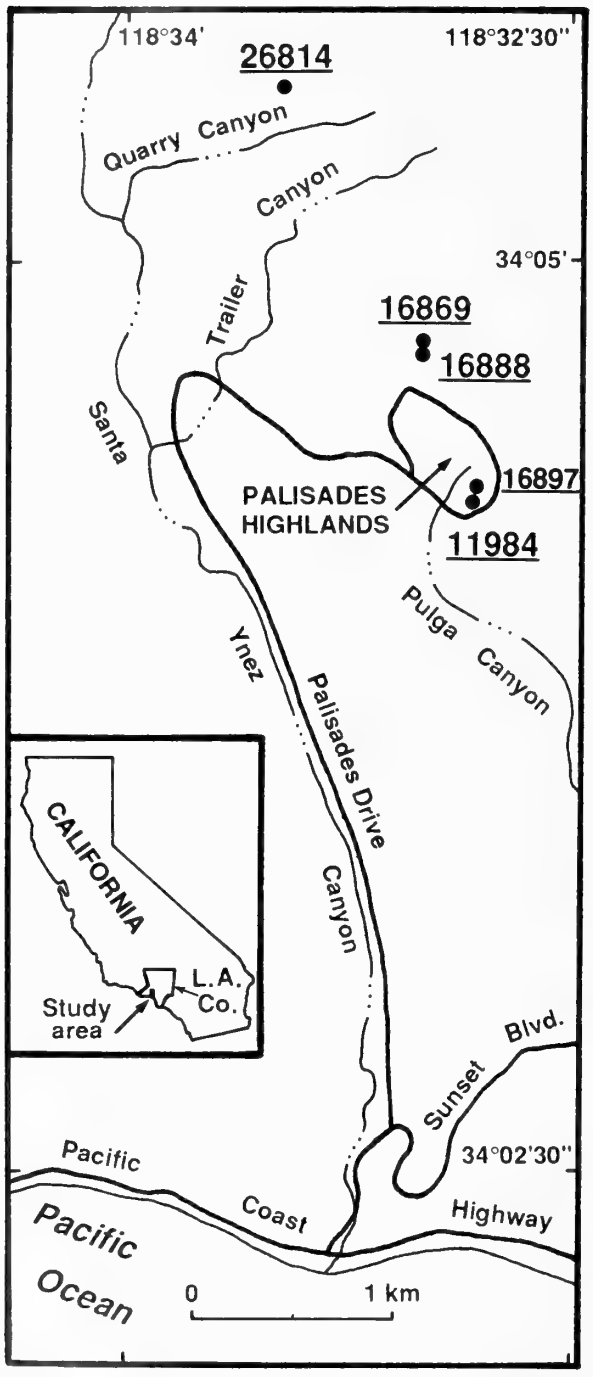


Figure 1

Index map showing LACMIP collecting localities in the upper Santa Susana Formation, Palisades Highlands and vicinity, east–central Santa Monica Mountains, Los Angeles County, southern California. Base map from Dibblee (1992).

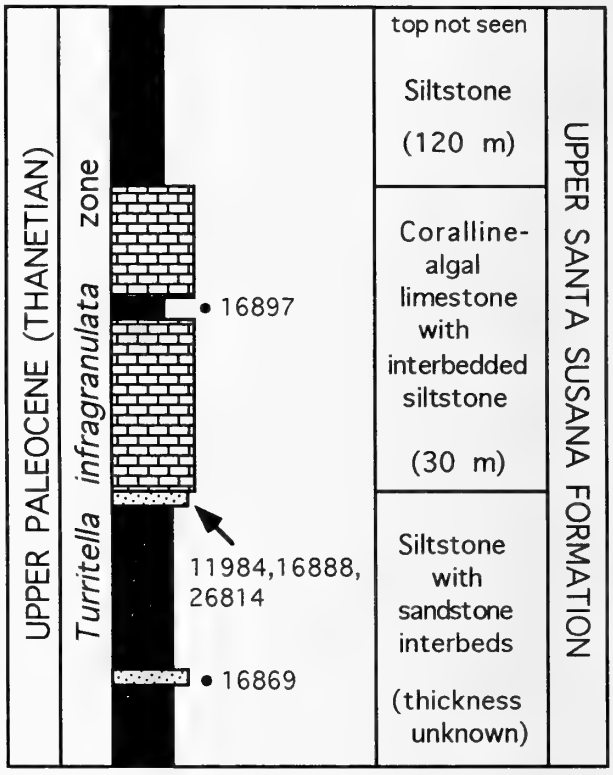


Figure 2

Generalized columnar section showing relative stratigraphic positions of the cited megafossil localities in the upper Santa Susana Formation in the Palisades Highlands and vicinity, east-central part of the Santa Monica Mountains, southern California.

Recent reconnaissance work by the senior author to resolve the algal-limestone problem in the immediate study area was uninformative because all of the outcrops had been obliterated by extensive housing-tract development. Pending future information, it seems best to refer to the algal limestone(s) as the "algal-limestone interval." Although the exact stratigraphic position of this interval is not known because structural complications make it impossible to identify the upper contact of the Santa Susana Formation, the interval is approximately 120 m below the stratigraphically highest outcrops of the Santa Susana Formation in the area (Mack, 1993).

The mollusks described in this report were collected from rocks stratigraphically near or within the algal-limestone interval, and their positions are shown in Figure 2. The pholadid bivalve *Martesia* sp. and the teredinid bivalve *Nototeredo*(?) sp. are from a richly fossiliferous lens within the gray-green very fine-grained sandstone at LACMIP loc. 16869 (Figures 1,2). This lens is approximately 20 m below the algal-limestone interval. The fauna at this locality is much more diverse than those from other units and yielded numerous specimens of the bi-

valves *Cucullaea mathewsonii* Gabb, 1864, *Crassatella unioides* (Stanton, 1896), *Saulella undulifera* (Gabb, 1869), and *Pholadomya* (*P.*) *nasuta* Gabb, 1864, and the gastropods *Turritella infragranulata* Gabb, 1864, and various species of naticids. A few small specimens of the solenid bivalve *Solena* (*Eosolen*) *stantoni* were also present.

The two gastropods treated herein are from fine-grained sandstone immediately subjacent to the algal limestone and are from slightly higher in the stratigraphic section than where *Martesia* and *Nototeredo* were found. Most of the specimens of the fissurellid gastropod *Diodora* sp. nov.? were found at LACMIP loc. 16888. One other specimen of *Diodora* sp. nov.? was found at LACMIP loc. 11984, and a single specimen of the potamidid gastropod *Terebralia* ***susana*** sp. nov. was found at LACMIP loc. 26814 in the Quarry Canyon area and below an algal limestone that Dibblee (1992) mapped as the only algal limestone in that area. This specimen of *Terebralia* ***susana*** is somewhat worn.

The largest and best preserved specimens of the solenid bivalve *Solena* (*Eosolen*) *stantoni* are from gray-green muddy silstone in the upper Pulga Canyon area at LACMIP loc. 16897. This siltstone appears to be a major interbed within the algal-limestone interval and, if so, would be slightly higher stratigraphically than the other discussed mollusks. Unfortunately, there have been no detailed stratigraphic sections in the critical area of upper Pulga Canyon where Dibblee's (1992) geologic map shows four vertically stacked lenses of algal limestone with intervening, mostly fine-grained siliciclastic units that dip consistently to the southwest. This is the only area where there are more than two vertically stacked outcrops of algal limestone, and this is the area where there has been extensive housing-tract construction since about 1988. The homes now make up the Summit and Enclave communities of Palisades Highlands in the city of Los Angeles. The siltstone at LACMIP loc. 16897 might represent a landslide or fault block and is from the same stratigraphic level as LACMIP loc. 16869. The siltstone at locality 16987, however, is muddier and has yielded a less diverse megafauna. In this paper, the siltstone at locality 16897, where the large *S.* (*E.*) *stantoni* specimens were found, will be considered tentatively as being within the algal-limestone interval.

The fossils in the muddy siltstone at LACMIP loc. 16897 are in poorly defined lentils containing bivalves and some gastropods. Three specimens of *S.* (*E.*) *stantoni* were found. Their valves are open and positioned next to each other in parallel fashion, with the anterior and posterior ends matching each other ("butterflied"). The specimens also lie parallel to the original bedding. Other bivalves here include *Nuculana* sp., a thin-shelled *Ostrea* sp., and *Venericardia* sp. Some of these bivalves are complete and are partially to completely closed, whereas others are unbroken single valves. Gastropods are represented by a few large specimens of *Turritella infragranulata* Gabb, 1864, (very near to *T. i. pachecoensis* Stanton, 1896, fide L. R. Saul, personal communication) and some small specimens of *Tornatellaea pinguis* (Gabb, 1864).

DEPOSITIONAL ENVIRONMENT

Colburn et al. (1988) and Colburn (1996) concluded that the upper part of the Santa Susana Formation in the Santa Ynez Canyon area was deposited in a low-energy protected bay, no deeper than 40 m, with the bay situated behind a barrier bar. They based their conclusion on the following: condition of the megafossils, fine grain size of the deposits, presence of well-developed horizontal laminae within the deposits, and lack of sedimentary structures associated with strong wave or current action. Their megafossil evidence consists of articulated bivalve shells, both adult and juvenile specimens of the same species, and absence of both preferred orientation and current-size sorting of the shells. They also concluded that branching calcareous algae developed shoals on the bay floor.

Strathearn et al. (1988) concluded that the upper part of the Santa Susana Formation in the Santa Ynez Canyon area accumulated in an unrestricted, muddy, middle-shelf environment near or below storm-wave base and no deeper than 70 m. They based their conclusions on the taxonomic composition of the dinoflagellates and benthic foraminifera in the deposits, as well as on the predominantly non-transported condition of the megafossils. They also concluded the algal limestones, which formed when there was interruption of the deposition of the terrigenous siliciclastics, represent *in situ* buildups in subtropical to tropical waters of about 20 m depth.

A relatively low-energy depositional environment is in keeping with the presence of complete and unabraded bivalves found associated with the bivalves treated herein. This is especially true for the "butterflied" condition of most of the specimens of *Solena* (*Eosolen*) *stantoni* found in siltstone at LACMIP loc. 16897 within the algal-limestone interval. Although "butterflied" specimens of bivalves can be transported, the distance of post-mortem transport cannot be great and the water cannot be too agitated; otherwise the valves will break apart. Modern solenids have a mostly tropical distribution and live from the intertidal zone to depths of 60–110 m; most species are found just below the low-water mark in the lower part of the intertidal zone or in shallow inner sublittoral depths (20–30 m) on the shelf. Some species live in coralline-algal sediment, whereas others live around mangroves (Von Cosel, 1990).

The other bivalves treated herein are not all that useful in paleoenvironmental studies. *Martesia* and *Nototeredo* are wood borers that live today in tropical to temperate seas (Turner, 1966; Cvancara, 1966, 1970). Their presence does not necessarily indicate proximity to land because drift wood can disperse widely in oceanic settings.

The two gastropods treated herein, and which were found immediately subjacent to algal limestone, belong to genera that one might expect to have lived in tropical to subtropical shallow-marine waters in the vicinity of algal-carbonate buildups. *Diodora*, a herbivorous gastropod that requires a hard substrate, is widespread today, ranging from cool-temperate to tropical waters. Along the Pacific Coast of North America only *D. aspera* (Rathke, 1833) lives north of California, and it is usually found intertidally on wave-swept rocky habitats. In California, *D. aspera* and *D. arnoldi* McLean, 1966, live subtidally (McLean, 1978). Species of *Diodora* show a greater diversity in the warmer waters of the Gulf of California to Peru, where they usually live in shallow subtidal settings (Keen, 1971). The specimens of *Diodora* found in the Santa Susana Formation are complete and do not show any signs of abrasion due to post-mortem transport.

Modern species of *Terebralia* are restricted to circumtropical regions that extend from eastern Africa to the western Pacific Ocean. They usually live in great numbers on fine substrate in brackish water on coastal mudflats in mangrove regions. Some specimens live on the roots of mangroves, and others live on intertidal sand and rocky habitats throughout the salt-marsh environment. Specimens can also be found in tidal channels, where they appear to have been washed in from adjacent environments (Houbrick, 1991). *Terebralia sulcata* Born, 1778, from throughout the western Pacific, is a hardy generalist and able to tolerate a wide range of substrate types and diet, with algae being one of its food sources. It can live in protected bays from which mangroves are absent (Houbrick, 1991). The single specimen of *Terebralia* found in the Santa Susana Formation is somewhat worn, indicating some post-mortem transport.

Another habitat-distinctive gastropod found just below algal limestone in the study area is *Campanile greenellum* Hanna & Hertlein, 1939, reported from the Santa Ynez Canyon area (i.e., Quarry Canyon and Trailer Canyon) by Squires (1993). *Campanile* is a primarily Old World Tethyan genus that is indicative of warm waters and very shallow depths.

AGE

Biostratigraphic age assignments for the Santa Susana Formation in the Santa Ynez Canyon area have previously relied upon mollusks, even though the megafauna is incompletely known. Early collections of mollusks were assigned to the Eocene (*sensu lato*) by Hoots (1931), but that was before the Paleocene Epoch was a formally recognized time interval. These "Eocene" mollusks are now widely regarded as mostly late Paleocene in age (e.g., Saul, 1983; Strathearn et al., 1988; Colburn et al., 1988; Dibblee, 1992). Saul (1983:fig. 8) restricted the algal limestones in the Coal Canyon Formation [= the Santa Susana Formation of herein] to the upper Paleocene *Turritella infragranulata* Zone, which is correlative to the European Thanetian Stage. The *T. infragranulata* Zone also corresponds to the Standard Planktonic Foraminferal Zone P4 (Saul, 1983) and to the upper part of the provincial "Martinez Stage" (Saul, 1983).

Our work also supports a late Paleocene age for the upper part of the Santa Susana Formation in the Santa Ynez Canyon area. The most useful locality in the study area for geologic age control is LACMIP loc. 16869, approximately 20 m downsection from the algal limestone (Figure 2). In addition to *Turritella infragranulata*, other age-diagnostic mollusks found at this locality include the gastropods *Prisoficus caudatus* (Gabb, 1869) and *Fulgoraria* (*Psephaea*) *zinsmeisteri* Mount, 1976, as well as the bivalves *Cucullaea mathewsonii, Crassatella unioides, Saulella undulifera,* and *Pholadomya* (*P.*) *nasuta*. These species are among the most characteristic species found in upper Paleocene rocks along the Pacific Coast of North America (Dickerson, 1914; Mount, 1976; Zinsmeister, 1983a; and Saul, 1983).

Most of the specimens of *Diodora* sp. nov.? were found at LACMIP loc. 16888, immediately below the algal limestone. The gastropod *Campanile greenellum* was also found at this locality, and it is confined to upper Paleocene rocks elsewhere in California (Squires, 1993).

At LACMIP loc. 11984, where a specimen of *Diodora* sp. nov.? was found immediately below the algal limestone, a fragmentary specimen of either a late form of *Turritella infragranulata pachecoensis* or an early form of *Turritella infragranulata* sensu stricto was found. At LACMIP loc. 16897, where specimens of *Solena* (*Eosolen*) *stantoni* were found in the middle of the algal-limestone interval (Figure 2), this same turritellid is also present. This turritellid indicates a late Paleocene (middle Thanetian) age (L. R. Saul, personal communication). The bivalve *Solena* (*Eosolen*) *stantoni* also indicates this age, as it is found elsewhere in California in rocks of late Paleocene age (Weaver, 1905; Dickerson, 1914; Zinsmeister, 1983a). This present study, therefore, shows that all the available megafossil evidence indicates that mollusks found near and immediately associated with algal limestones are late Paleocene in age.

Benthic foraminiferal, dinoflagellate, and pollen studies of the Santa Susana Formation in the study area have yielded conflicting geochronologic results. Mack (1993) reported benthic foraminifers that indicated the entire algal-limestone interval to be upper Paleocene, although the overlying rocks in the Santa Susana Formation might also range into the lower Eocene. Mack (1993) and Mack & Colburn (1993) reported also that benthic foraminifers indicate the Paleocene/Eocene boundary to be within the algal-limestone interval but did not discuss their reasoning.

Strathearn et al. (1988), based on dinoflagellate and pollen studies, suggested that the Paleocene-Eocene boundary might be several meters below the algal-lime-

stone interval, but this determination was based on a single genus of fungal spore, whose geologic range is somewhat open to question and primarily based on specimens in nonmarine outcrops in the continental interior. If Strathearn et al. (1988), Mack (1993), and Mack & Colburn (1993) are correct, then the molluscan fauna in the algal limestone and younger parts of the Santa Susana Formation in the Santa Ynez Canyon area should contain species found in the provincial molluscan "Meganos Stage" that overlies the upper Paleocene "Martinez Stage." There is no molluscan evidence to support this conclusion. The molluscan fauna associated with the algal limestones in the Santa Ynez Canyon area is unlike that from "Meganos Stage" strata in the upper part of the Santa Susana Formation on both the north and south sides of Simi Valley, 27 km northwest of the Santa Monica Mountains (Squires, 1991).

Strathearn et al. (1988:table 3) also reported the gastropod *Mesalia clarki* (Dickerson, 1914) in rocks they considered to be within the lower Eocene part of the Santa Susana Formation in the Trailer Canyon area (Figure 1). A study of the collections at LACMIP revealed this species to be in strata immediately below, and possibly within, the single algal-limestone exposure mapped in this area by Dibblee (1992). *Mesalia clarki* was known previously only from its type locality in the upper Paleocene Martinez Formation on the north side of Mount Diablo, northern California.

In summary, the age of the molluscan fauna discussed herein is considered to be late Paleocene (Thanetian). There is no molluscan evidence, nor is there any compelling microfossil evidence, to support a younger, early Eocene age for the Santa Susana Formation in the eastern Santa Monica Mountains.

SYSTEMATIC PALEONTOLOGY

Class GASTROPODA Cuvier, 1797

Order VETIGASTROPODA Salvini-Plawén, 1980

Family FISSURELLIDAE Fleming, 1822

Genus *Diodora* Gray, 1821

Type species: *Patella apertura* Montagu, 1803 [= *Patella graeca* Linnaeus, 1758], by original designation; Recent, British Isles.

Diodora sp. nov.?

(Figures 3–5)

Description: Shell medium in size (up to 3.4 cm in length and 5 mm in height), profile low, height about one-sixth of length, base flat, aperture oval. Apex situated slightly anterior to middle of shell. Anterior slope slightly steeper than posterior slope. Perforation moderately large, just anterior of apex, anterior end of perforation rounded, posterior end narrower. Interior apertural callus truncate posteriorly. Sculpture shown on internal mold consists of numerous closely spaced, equal strength primary radial ribs originating at apex; ribs slightly stronger near ventral margin. Stronger radial ribs alternate with slightly weaker ones on posterior slope. Concentric ornamentation weak, imparting a minute cancellate pattern on shell.

Distribution: Upper part of Santa Susana Formation, Pulga Canyon area, east-central Santa Monica Mountains (LACMIP locs. 11984 and 16888).

Geologic age: Late Paleocene (Thanetian).

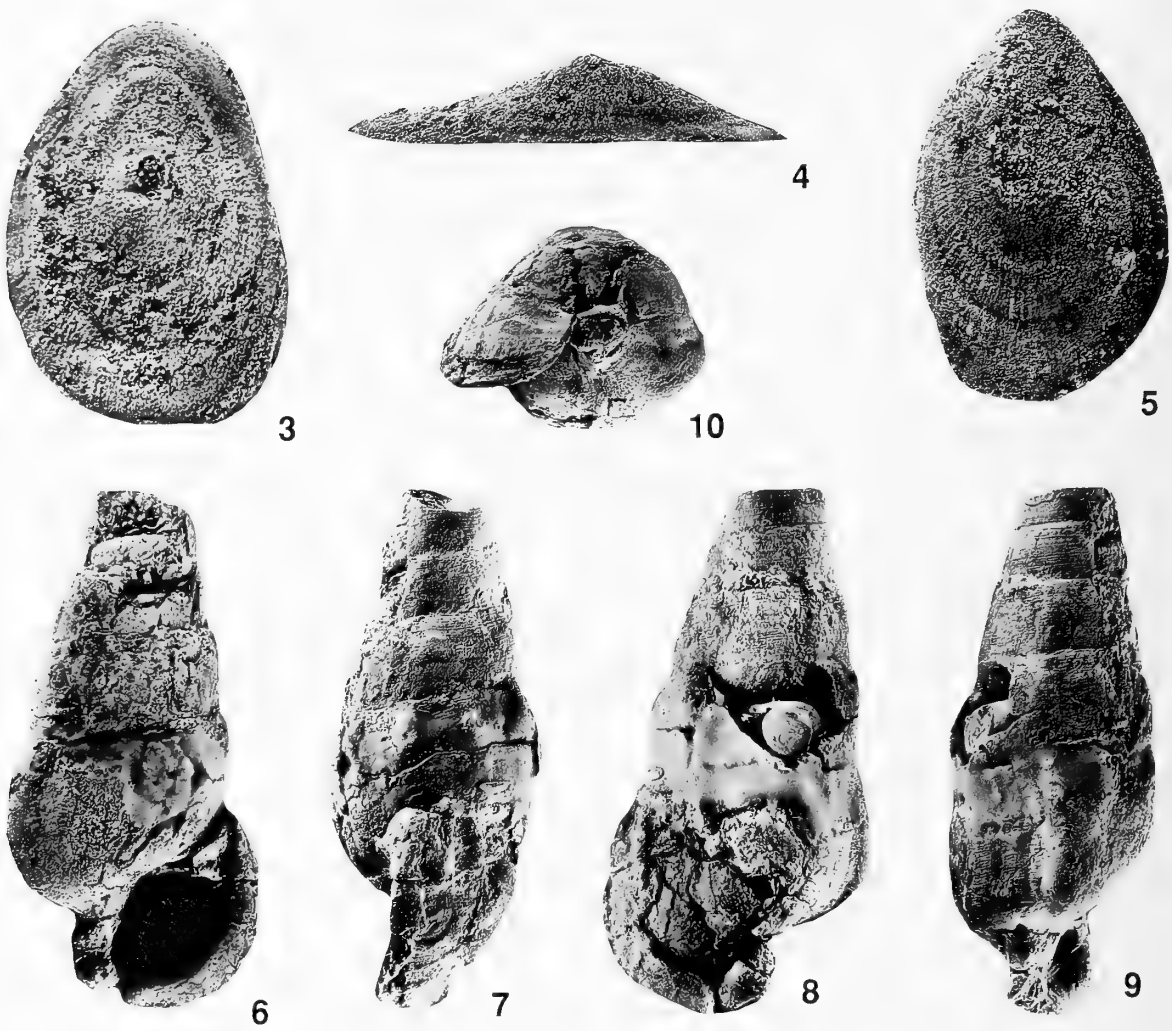
Discussion: Eight specimens were found, seven from LACMIP loc. 16888 and an eighth from LACMIP loc. 11984, all from sandstone directly below the algal limestone.

All the specimens of *Diodora* sp. nov.? are essentially internal molds of complete individuals, but they have taken on the impression of external ornamentation, and thus are functional casts. Although the specimens probably represent a new species, their poor preservation prevents confirmation of such. Only one specimen (Figure 3) shows evidence of the truncate internal callus that is diagnostic of *Diodora*.

The specimens of *Diodora* sp. nov.? from the upper Santa Susana Formation represent the earliest known specimens of *Diodora* from the Pacific Coast of North America. The genus has been reported from Paleocene and Eocene rocks in the eastern and southeastern United States (Palmer & Brann, 1966). Wenz (1938) and Keen (1960) reported the geologic range of *Diodora* to be Late Cretaceous to Recent. Sohl (1992) noted that Cretaceous species of so-called *Diodora* are very rare and that the generic status of most of them is open to question. Two of the earliest known species that can be assigned positively to *Diodora* are from Upper Cretaceous (Maastrichtian Stage) strata, from Puerto Rico and Jamaica (Sohl, 1992).

The Santa Susana Formation specimens most closely resemble specimens of *Diodora* sp. aff. *D. stillwaterensis* (Weaver & Palmer, 1922) of Squires & Deméré (1991: figs. 3A, B) from the middle Eocene ("Transition Stage") Friars Formation in San Diego County, southern California, but differs in having fewer primary radial ribs and in having secondary radial ribs on the posterior slope.

Only two Paleogene species of *Diodora* have been described from the Pacific Coast of North America. One is *Diodora stillwaterensis* (Weaver & Palmer, 1922:27, pl. 11, figs. 3, 6; Weaver, 1942 [1943]:284, pl. 63, fig. 20; pl. 64, figs. 4, 7, 12), from the Cowlitz Formation of Lewis and Cowlitz Counties in western Washington, which Nesbitt (1995) has assigned to the upper middle Eocene. The Santa Susana Formation specimens differ from *D. stillwaterensis* by having a larger shell, a lower profile, secondary radial ribs confined to the posterior re-



Explanation of Figures 3 to 10

All specimens coated with ammonium chloride. Figures 3–5. *Diodora* sp. nov.?, LACMIP loc. 16888. Figures 3–4. LACMIP hypotype 7940, length 33.2 mm, height 5 mm. Figure 3. dorsal view of internal mold, ×1.6. Figure 4. left-lateral view of internal mold, ×1.7. Figure 5. LACMIP hypotype 7941, length 26.9 mm, dorsal view of internal mold, ×1.9. Figures 6–10. *Terebralia* ***susana*** Squires & Kennedy, sp. nov., LACMIP holotype 7942, LACMIP loc. 26814, length 65 mm (incomplete), width 31.7 mm, ×1.1, low-level lighting used to show subdued sculpture. Figure 6. apertural view. Figure 7. right-lateral view. Figure 8. apertural view. Figure 9. left-lateral view. Figure 10. anterior view.

gion, and lack of tertiary radial ribs. Comparison with the holotype (UWBM 194) of *D. stillwaterensis* is not possible because the specimen is missing (R. C. Eng, personal communication).

The second Paleogene *Diodora* is *D. batequensis* Squires & Demetrion (1994:127, 129, figs. 3–6) from the middle lower Eocene ("Capay Stage") part of the Bateque Formation in the eastern Laguna San Ignacio area of Baja California Sur, Mexico (Squires & Demetrion, 1994). The Santa Susana Formation specimens differ from *D. batequensis* by having a larger shell, a lower profile, many fewer and much weaker primary radial ribs, secondary ribs confined to posterior region, a lack of tertiary radial ribs, and weaker concentric sculpture.

Squires & Goedert (1994a: 15, fig. 28) reported poorly preserved internal molds of *Diodora* sp. indet. from sandstone interbedded with basalt flows in the middle lower Eocene ("Capay Stage") part of the upper Crescent Formation in the Little River area, southwestern Washington. Similarly poorly preserved specimens of *Diodora* sp. indet. are also present in coralline algae-rich sandstone interbedded with basalt flows at CSUN loc. 1563 in the upper Crescent Formation at Larch Mountain, Black

Hills, near Olympia in southwestern Washington (Squires & Goedert, 1994b).

Superorder CAENOGASTROPODA Cox, 1959

Order NEOTAENIOGLOSSA Haller, 1882

Superfamily CERITHIOIDEA Férussac, 1819

Family POTAMIDIDAE Adams & Adams, 1854

Genus *Terebralia* Swainson, 1840

Type species: *Strombus palustris* Linnaeus, 1758, by subsequent designation (Sacco, 1895); Recent, tropical waters, eastern Africa to western Pacific Ocean.

*Terebralia **susana*** Squires & Kennedy, sp. nov.

(Figures 6–10)

Diagnosis: *Terebralia* whose adult whorls have numerous weak, very closely spaced spiral threads and about 11 axial ribs.

Description: Shell large in size, 6.5 cm high (incomplete, upper spire missing; projected height about 9.5 cm), thick-shelled; turreted-conical, consisting of at least five whorls. Upper spire unknown. Whorls convex, suture distinct and slightly inset into each successive whorl. Last five whorls with numerous weak, very closely spaced spiral threads; body whorl near outer lip with widely spaced, coarse spiral ribs, about seven in number, decreasing in strength anteriorly and with three spiral ribs in interspaces. Last three whorls with axial ribs (indeterminate in number, estimated to be about 11 per whorl), most strongly developed on posterior half of whorl. Last three whorls with aligned varices on both sides of shell. Base of body whorl rounded. Aperture large, ovate, with a posterior groove; anterior siphonal canal short and nearly closed at junction with outer lip. Inner lip smooth, concave. Outer lip flared, with varix; interior of outer lip smooth.

Holotype: LACMIP 7942.

Type locality: LACMIP loc. 26814, upper part of Santa Susana Formation, upper Quarry Canyon, east-central Santa Monica Mountains, latitude 34°05′24″N, longitude 118°33′30″W.

Dimensions: Height 65 mm (incomplete), width 31.7 mm.

Distribution: Known only from the type locality (LACMIP loc. 26814).

Geologic age: Late Paleocene (Thanetian).

Discussion: Only a single specimen was found at LACMIP loc. 26814, in sandstone immediately below the algal limestone. The specimen is somewhat worn and the upper spire is missing. No other megafossils were found in association with the holotype at the type locality.

*Terebralia **susana*** is very similar to *T. pathani* Iqbal (1969:20, pl. 12, figs. 11–12) from littoral to sublittoral mudstone of the lower Eocene Ghazij Formation east of Quetta in Pakistan, but *T. **susana*** differs by having a larger shell, weak and closely spaced spiral threads on adult whorls, and fewer, weaker, and more widely spaced spiral ribs near the outer lip.

A tentatively identified terebralid, *Terebralia? juliana* Dailey & Popenoe (1966:22, pl. 6, figs. 7, 8) from the Upper Cretaceous (upper Campanian Stage to lower Maastrichtian Stage) Jalama Formation in Santa Barbara County of southern California, represents what may be the only other report of this genus from the Pacific Coast of North America. *Terebralia **susana*** differs from *T. juliana* by having a much larger and thicker shell, poorly developed spiral ribbing rather than four well-developed spiral ribs bearing numerous prominent nodes, and axial ribbing.

According to Houbrick (1991), the geologic range of *Terebralia* is early Miocene to Recent. Cossmann (1906) and Wenz (1940), however, cited the genus from rocks as old as Late Cretaceous (Maastrichtian Stage). Pervinquière (1912:pl. 1, figs. 26–28) reported specimens of *Cerithium* (*Terebralia*) *sanctiarromani* Thomas et Peron, 1889, from slightly older, Turonian (Upper Cretaceous) rocks in Tunisia, northern Africa. Positive generic assignment of that particular species cannot be made because the aperture is unknown. The shell does resemble that of *Terebralia*. *Terebralia **susana*** differs from the Tunisian species by having many fewer axial ribs.

Etymology: The species is named for the Santa Susana Formation.

Class BIVALVIA Linnaeus, 1758

Order VENEROIDA Adams & Adams, 1856

Family SOLENIDAE Lamarck, 1809

Genus *Solena* Mörch, 1853

Type species: *Solen obliquus* Spengler, 1794, by subsequent designation (Stoliczka, 1871); Recent, Caribbean Sea.

Subgenus *Eosolen* Stewart, 1930

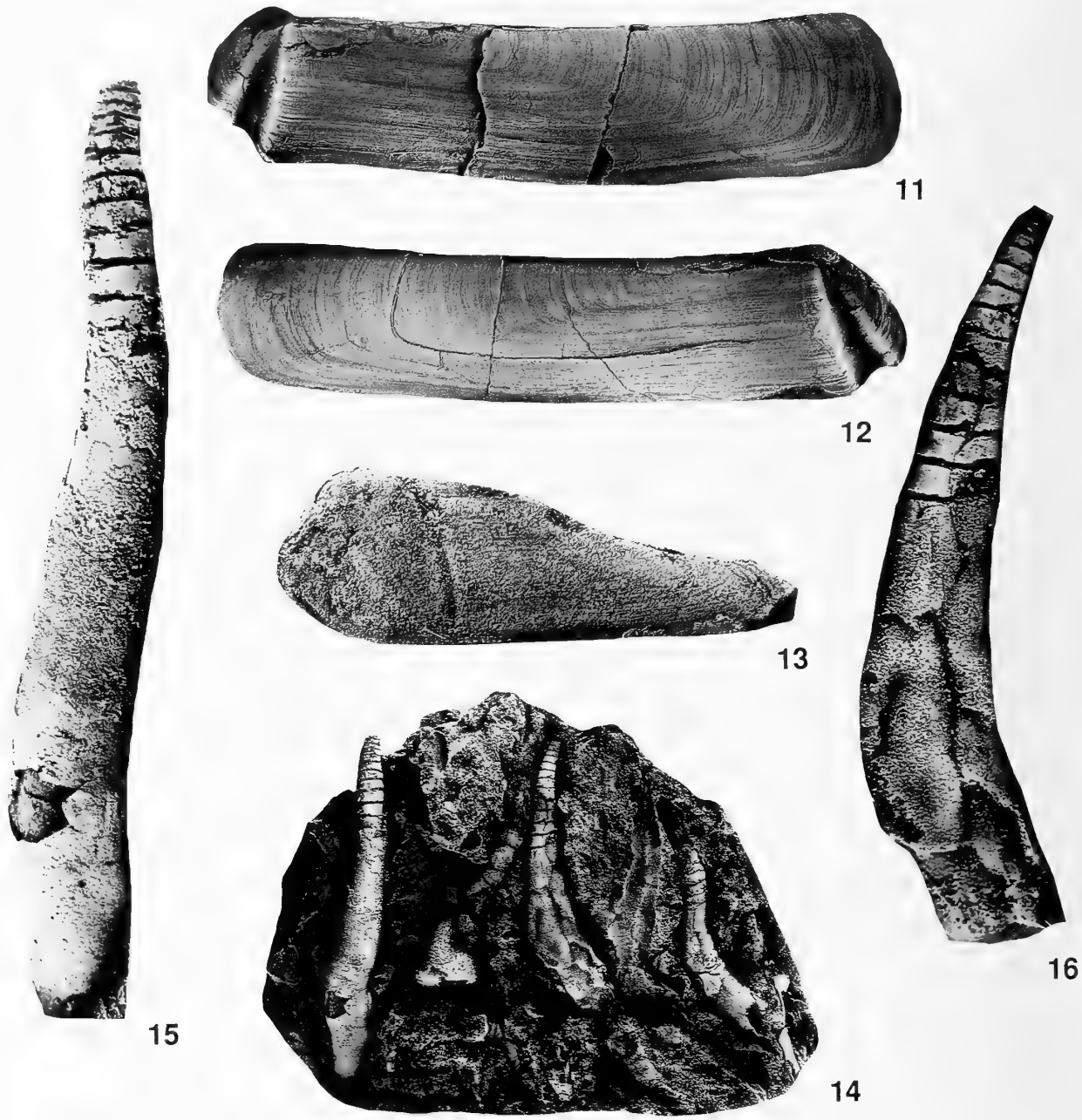
Type species: *Solen plagiaulax* Cossmann, 1906, by original designation; middle to upper Eocene (Lutetian to Bartonian Stages), Paris Basin, France.

Solena (*Eosolen*) *stantoni* (Weaver, 1905)

(Figures 11–12)

Solen stantoni Weaver, 1905:116, pl. 12, fig. 1. Dickerson, 1914:151 (table), pl. 12, fig. 3. Keen & Bentson, 1944: 108.

Solena (*Eosolen*) *stantoni* (Weaver). Zinsmeister, 1983a:63 (table), pl. 1, fig. 18.



Explanation of Figures 11 to 16

Figures 11–12. *Solena* (*Eosolen*) *stantoni* (Weaver, 1905), LACMIP hypotype 7943, LACMIP loc. 16897, closed-valve specimen, length 65 mm, height 15 mm, ×1.6. Figure 11. left valve. Figure 12. right valve. Figure 13. *Martesia* sp., LACMIP hypotype 7944, LACMIP loc. 16869, internal mold of left valve, length 33.8 mm, height 11.4 mm, ×2.4. Figures 14–16. *Nototeredo*(?) sp., LACMIP hypotype 7945, LACMIP loc. 16869. Figure 14. hand specimen of a cluster of individuals, two of which are shown in the following figures, ×1.3. Figure 15. side view of individual on left side of hand specimen, height 45 mm, maximum width 4.9 mm, ×3.2. Figure 16. side view of individual in center of hand specimen, height 32 mm, maximum width 6 mm, ×3.5

Not *Solen* (*Plectosolen*) *stantoni* Weaver. Clark & Woodford, 1927:103–104, pl. 18, fig. 10.

Not *Solen* cf. *parallelus* Gabb. Clark & Woodford, 1927: 104, pl. 18, fig. 9 [=*Solen* (*Plectosolen*) *stantoni* (Weaver), *in errata* fide Keen & Bentson, 1944].

Original description: "The shell is thin, elongated and moderately convex. The cardinal and basal margins are nearly parallel. The beaks are anterior. The base is straight and the ends somewhat rounded. The posterior end is more abruptly truncated than the anterior. The surface is marked by faint concentric lines of growth. Passing down from the beak to the base of the anterior margin there is on each side a deep, sharp constriction which is nearly at right angles to the hinge line. The maximum length of the type specimen was found to be 50 mm. The greatest width is 7 mm" (Weaver, 1905:p. 116).

Supplementary description: Shell moderately large in size, up to 6.6 cm in length, shell thin, elongate, ornamented by concentric growth lines; dorsal and ventral margins nearly parallel, dorsal margin slightly concave; beaks anterior; posterior end somewhat truncate; anterior area on both valves separated from remainder of shell by a deep and wide umbonal groove, widest at the ventral margin, set at an angle of about 105 to 110° to the dorsal margin; a distinct ridge and a second weaker, groove lie parallel and immediately anterior to the primary umbonal groove; anterior end produced, gaping, and bent posteriorly. Dentition unknown.

Holotype: UCMP 11941.

Type locality: UCMP loc. 532, upper Vine Hill Sandstone between Martinez and Walnut Creek at mouth of Vaca Canyon, Contra Costa County, northern California.

Geographic distribution: Contra Costa County, northern California to Santa Monica Mountains, Los Angeles County, southern California.

Geologic age: Late Paleocene (Thanetian).

Stratigraphic distribution: Upper Vine Hill Sandstone, near Pacheco, Contra Costa County (Weaver, 1953); middle part of Santa Susana Formation, south side of Simi Valley, Ventura County (Zinsmeister, 1974, 1983a); upper part of Santa Susana Formation, Santa Ynez Canyon area (LACMIP loc. 16869), east-central Santa Monica Mountains; upper part of Santa Susana Formation in Pulga Canyon (LACMIP loc. 16897), east–central Santa Monica Mountains.

Discussion: The subgenus *Eosolen* is characterized by having an oblique umbonal groove on the anterior end.

Two small specimens of *S.* (*E.*) *stantoni* were found at LACMIP loc. 16869 in the Santa Ynez Canyon area. One is an external mold of a complete late-juvenile specimen (20 mm long and 6 mm high) that consists of an open pair of valves, arranged in parallel fashion immediately next to each other ("butterflied"). The second specimen is a fragment of a slightly larger individual. Three large specimens were also found at LACMIP loc. 16897 in the upper Pulga Canyon area. These are complete, early to late adult, ranging from 5.5 to 6.6 cm in length and 13 to 15.5 mm in height, and they represent the largest known specimens of this species. Each consists of an open and "butterflied" pair of valves. Only the exteriors are visible. The specimens are essentially internal molds, but have impressions of the exterior sculpture, and thus are functional casts. Tiny remnants of the original shell material remain in a few places.

Both juvenile and adult specimens of *Solena* (*Eosolen*) *stantoni* are alike in their morphologic features in that they all have a slightly curved dorsal margin and a produced anterior end with two grooves. Morphologically they resemble the holotype but are better preserved. The holotype is a closed-valved early adult (length 5 cm) whose shell is mostly decorticated.

Clark & Woodford (1927:103–104, pl. 18, fig. 10 = UCMP hypotype 31324) illustrated a specimen of *Solen* (*Plectosolen*) *stantoni* (Weaver) from "division D strata of the Meganos Formation" in Deer Valley, Contra Costa County, northern California. Almgren et al. (1988:fig. 4) assigned "division D strata of the Meganos Formation," as used by Clark & Woodford (1927), to the CP9 Zone (lowest Eocene) of the standard calcareous nannofossil zonation. These shallow-marine strata are now referred to the Margaret Hamilton Sand (Edmondson, 1984). Clark & Woodford (1927:104, pl. 18, fig. 9 = UCMP hypotype 31325) also illustrated another specimen from the same formation as *Solen* sp. cf. *parallelus* Gabb. According to Stewart (1930) and Keen & Bentson (1944), Clark & Woodford noted *in errata* that UCMP hypotype 31325 should have been identified as *S.* (*Plectosolen*) *stantoni*. Examination of the two hypotypes reveals that they are unlike *S.* (*E.*) *stantoni* because the dorsal margin of each is straight rather than slightly curved and the anterior end of each is too rounded. The hypotypes of Clark & Woodford (1927) are herein tentatively identified as *Solena* (*E.*) *subverticala* Vokes (1939:96–97, pl. 15, fig. 8), which is known from the middle lower Eocene ("Capay Stage") to middle Eocene ("Domengine Stage") rocks in southern California (Givens, 1974), and from "Domengine" rocks in central California (Vokes, 1939).

Keen (1969) and Davies & Eames (1971) reported that *Eosolen* was restricted to the Eocene of Europe and North America. The lower limit of the geologic range is revised to late Paleocene by the presence of *Solena* (*Eosolen*) *stantoni* in upper Paleocene rocks in California.

The only other Paleocene solenid of which we are aware is "*Solen*" *parallelus* Gabb (1864:146–147, pl. 22, fig. 117), the lectotype of which is not well preserved, especially anteriorly. "*Solen*" *parallelus* was also figured by Stewart (1930:291–292, pl. 7, fig. 1), who reported that there is a faint suggestion of a diagonal groove on the anterior end. The type locality of "*S.*" *parallelus* is

controversial, and the species has been confused with Eocene solenids from the Pacific coast of North America. The type locality of "*S.*" *parallelus* is most likely from the Martinez area in Contra Costa County of northern California and is from upper Paleocene rocks (Stewart, 1930; Keen & Bentson, 1944). Due to poor preservation of existing material, this species is not assignable to a subgenus. *Solena* (*Eosolen*) *stantoni*, therefore, is the only confirmed representative of *Eosolen* in the Paleocene.

"*Solen*" *cuneatus* Gabb (1869:175–176, pl. 29, fig. 61), possibly from Cretaceous rocks near the Martinez area, is very poorly preserved (Stewart, 1930:292, pl. 5, fig. 12), and the confirmation of its solenid status (which seems doubtful) awaits better preserved material.

Dailey & Popenoe (1966) reported a late Campanian or possibly early Maastrichtian *Leptosolen* sp. from the Jalama Formation in Santa Barbara County of southern California. *Leptosolen* Conrad, 1867, resembles *Eosolen* but is characterized by wider valves, less terminal beaks, and the presence of a strong internal rib, and, in some species, with concentric imbricating sculpture (Conrad, 1867; Stephenson, 1941; Dailey & Popenoe, 1966). *Leptosolen*, which is known only from the Cretaceous and is widely distributed, belongs to the family Cultellidae, which is closely related to family Solenidae (Keen, 1969). *Leptosolen* sp. from the Jalama Formation is represented by a few internal molds, and examination of the best specimens (LACMIP hypotypes 40425 and 40426) reveals that they might belong to *Eosolen*. They are similar to *Eosolen* in narrow valves, and the beaks are more anterior than on *Leptosolen*. In addition, the internal molds show a sulcus on each valve that resembles the anterior umbonal groove of *Eosolen* in that it is nearly vertical and close to the end of the shell. If the sulcus had been formed by the diagnostic internal rib of *Leptosolen*, it would be nearer the center of the shell. Better preserved specimens of *Eosolen*-like shells from the Jalama Formation are needed to confirm their generic assignment. If they do prove to belong to *Eosolen*, they would represent its earliest record.

Order MYOIDA Stoliczka, 1870

Family PHOLADIDAE Lamarck, 1809

Subfamily MARTESIINAE Grant & Gale, 1931

Genus *Martesia* Sowerby, 1824

Type species: *Pholas clavata* Lamarck, 1818 [= *Martesia striata* (Linnaeus, 1758)], by original monotypy; Recent, "seas of Western Europe and America" (Turner, 1955).

Martesia sp.

(Figure 13)

Description: Small to medium in size, reaching approximately 3.4 cm in length and 1.5 cm in height, elongate, pear-shaped and tapering posteriorly. Umbones near anterior end. Shell divided by umbonal-ventral sulcus extending obliquely and posteroventrally from umbo to ventral margin. Anterior slope broad, rounded, with broad V-shaped notch on growth margin, about one-third of entire shell length; anterior slope sculptured by fine, concentric ridges, too finely denticulated to express radial sculpture. Disc and posteror slope with numerous, closely spaced, fine concentric ridges. Callum smooth, entire, without ellipsoidal notch on margin. Funnel-shape pit below umbonal reflection present on one specimen. Umbonal regions on all specimens too poorly preserved for description. Accessory plates lacking.

Distribution: Upper part of Santa Susana Formation, Santa Ynez Canyon area (LACMIP loc. 16869), east-central Santa Monica Mountains.

Geologic age: Late Paleocene (Thanetian).

Discussion: Fossil specimens of the wood-boring genus *Martesia* are rare in Paleogene deposits of the Pacific Coast of North America (Kennedy, 1974:58). The six specimens recovered from the upper part of the Santa Susana Formation in the Santa Ynez Canyon area (LACMIP loc. 16869) represent only the fifth confirmed record of typical *Martesia* from the Pacific Coast region and, more significantly, they represent the earliest record for the genus in this region. Although the genus has been reported in Jurassic and Cretaceous rocks, all Mesozoic specimens thus far examined (by the junior author) are assignable to *Opertochasma* Stephenson, 1952, another wood-boring genus similar in some respects to *Martesia* (Kennedy, 1974).

The six specimens from the Santa Susana Formation in the Santa Monica Mountains are all isolated single valves of adults preserved in sandstone. Associated carbonaceous material and one small piece of wood suggest proximity to peaty, vegetative, or wood debris. It is probable that the isolated valves separated and dispersed following disintegration of their original water-logged woody substrate. The umbonal regions of all specimens are poorly preserved, and most of the original shell material is missing on the specimens. The posterior-dorsal margin of the figured specimen (Figure 13, LACMIP hypotype 7944) is crushed and folded out of view. Accessory plates, such as the mesoplax, metaplax, and hypoplax, that fit around the margins of the paired valves, and which are useful in species identification, were not preserved or recovered.

Species of *Martesia* all have similar elongate, pear-shaped valves, an anterior margin with a broad V-shaped notch, a funnel-shaped pit below the umbonal reflection, and a wood-boring habit that makes them readily identifiable at the generic level. Kennedy (1974) recognized three subgenera of *Martesia*. Two of these, *Martesia* sensu stricto and *Particoma* Bartsch & Rehder, 1945, are

distinguished by differences in their mesoplax (the dorsal accessory plate that fits above the umbones), in addition to characteristics of their umbonal regions. The posterior-dorsal margins of *Martesia* and *Particoma* are not reflected, as they are in the third subgenus, *Paramartesia* Kennedy, 1974, whose posterior-dorsal margin is folded over upon itself, forming an elongae enclosure similar to that found in the modern rock-boring genus *Parapholas* Conrad, 1848. The type species of *Paramartesia*, namely *Martesia* (*Paramartesia*) *tolkieni* Kennedy (1974:59–60, figs. 67–70, frontispiece), is from the Lodo Formation on the west side of the San Joaquin Valley in central California. The Lodo Formation ranges from upper Paleocene to lower Eocene, but the type locality of *M.* (*P.*) *tolkieni* plots in the upper part of the formation (Payne, 1974:pl. 1), thus placing it in the lower Eocene part of the formation. The Santa Ynez Canyon specimens of *Martesia* sp. differ from *M.* (*P.*) *tolkieni* by not having a reflected posterior-dorsal margin.

Martesia meganosensis Clark & Woodford (1927:103, pl. 18, figs. 7, 8; Kennedy, 1974:58–59, figs. 65, 66) from the Margaret Hamilton Sand [= division D of Meganos Formation as used by Clark & Woodford (1927)] in Contra Costa County of northern California, is the only described California Paleogene Martesia that actually belongs to "typical" *Martesia*. The type specimens (Kennedy, 1974:58–59, figs. 65, 66) of *M. meganosensis*, however, do not have any characters distinctive below the generic level, and thus the name should be considered a *nomen dubium*. Almgren et al. (1988:fig. 4) assigned "division D strata of the Meganos Formation," as used by Clark & Woodford (1927), to the CP9 Zone (lowest Eocene) of the standard calcareous nannofossil zonation.

Forty-two specimens of *Martesia* sp. cited by Hickman (1969:69, pl. 8, figs. 4, 6) from the Eugene Formation near Eugene, Oregon, belong to *Martesia* sensu stricto based on the mesoplax of several specimens preserved in a single piece of fossil wood. Kennedy (1974:58) also reported one small, poorly preserved specimen of *Martesia* sp. from the Keasey Formation at Rock Creek, near Keasey, northwestern Oregon. Armentrout et al. (1983) assigned both the Eugene Formation and the Keasey Formation to the upper Eocene.

Other Paleogene records of *Martesia* from the Pacific coast lower Tertiary are more properly assigned to other genera. As reported by Kennedy (1974:61), Nelson's (1925:facing p. 402) record of "*Martesia* (?) species" from the "Martinez marine member" on the south side of Simi Valley in Ventura County, southern California, was based on a single poorly preserved specimen that is probably assignable to *Opertochasma*. Zinsmeister (1983a, 1983b) and Saul (1983:94) assigned the "Martinez marine member" to the Paleocene (Thanetian).

Martesia turnerae Hickman (1969:68, pl. 8, figs. 10–11, 13–14, 16), from the upper Eocene Eugene Formation in Oregon is also an *Opertochasma*, as demonstrated by Kennedy (1974:61, figs. 71–72).

"*Martesia*(?) sp." of Dickerson (1914:96, 140; see Kennedy, 1974:72, fig. 99), from the Paleocene Martinez Formation at Little Lake in Lake County of northern California, can be assigned to *Teredina* Lamarck, 1818, (Kennedy, 1974; S. R. A. Kelley, personal communication). *Teredina* is well represented and best known from the Eocene of the Paris Basin, France.

Family Teredinidae Rafinesque, 1815

Subfamily Bankiinae Turner, 1966

Genus *Nototeredo* Bartsch, 1923

Type species: *Teredo edax* Hedley, 1895, by original designation; Recent, Australia and New Zealand.

Nototeredo(?) sp.

(Figures 14–16)

Description: A cluster of seven calcareous tubes, either separate or touching, up to 4.5 cm in length and 6 mm in diameter; gently to moderately curved, tapered posteriorly. Tubes without constrictions, except at the concamerate posterior (siphonal) end. Concamerate part about 25 to 40 percent of length of tubes (incomplete); consisting of 10 to 12 concentrically arranged, internal restrictions (concamerations) that are spaced up to 1.5 mm apart.

Distribution: Upper part of Santa Susana Formation, Santa Ynez Canyon area (LACMIP loc. 16869), east-central Santa Monica Mountains.

Geologic age: Late Paleocene (Thanetian).

Discussion: A single hand specimen (Figure 14) containing a cluster of concamerate tubes was found at LACMIP loc. 16869. The specimens in Figure 14 are tubes that have been filled with sediment and subsequently leached (dissolved) away, leaving a cavity where the original shell once was. All the tubes in the cluster are oriented with the posterior ends (siphonal openings) in the same direction, indicative of their original aligned position within the enclosing substrate. Although teredinids are typically wood borers, the absence of preserved wood suggests they might have been colonizing an organic-rich, peaty substratum rather than wood.

The concamerate tubes at LACMIP loc. 16869 resemble those belonging to genus *Nototeredo* Bartsch, 1923, and as far as we know, this is the only genus to have tubes similar to those from the Santa Susana Formation. Nevertheless, a positive identification cannot be made because the valves of the shell are missing, as are the pallets, which are used for generic and species identification, at least among modern teredinids (Turner, 1966). On the basis of figure 13D of Turner (1966:39), one could infer

that the concamerations are designed to fit closely around the extended siphons in wider, down-hole parts of the tube that accommodate other organs or structures, but which are otherwise too cavernous for the slender siphons.

The tubes closely resemble those of *Nototeredo globosa* (Meek & Hayden, 1858:53; Meek, 1876:264–265, figs. 31, 32 and pl. 30, fig. 13), a wood-boring teredinid from the upper Paleocene (Danian) Cannonball Formation from North Dakota. Cvancara (1970:620–621, pl. 121, fig. 12) illustrated the pallets and concamerate tubes of this species and noted that the tubes are present both in well-preserved petrified wood as well as in very fine-grained detrital rocks in which little, if any, original organic material remains. The Santa Susana Formation specimens differ by being more curved and more tapered, but this is probably related to the original substratum rather than being of taxonomic significance. The calcareous tubes of most wood-boring teredinids are of very little taxonomic use, and generic and specific determinations are typically based on the periostracal parts of the pallets, which are rarely preserved in the fossil record (Turner, 1966).

Similar concamerated tubes of "*Gastrochaena amphisbaena*" Goldfuss, 1837, have been illustrated by Geinitz (1874:pl. 52, figs. 8–12). Goldfuss' species is from the Pläner beds in southeastern Germany, which Gignoux (1950:421) assigned to the Upper Cretaceous (Cenomanian Stage to Turonian Stage). The Santa Susana Formation specimens differ from Goldfuss's specimens by their greater consistency in the spacing of the concamerate segments. In addition, none of the Santa Susana Formation specimens has the close spacing found in some of the German specimens, although the taxonomic significance, if any, of this spacing has not been evaluated.

Nototeredo(?) sp. from the Santa Susana Formation in the Santa Ynez Canyon area represents the first record of fossil concamerate tubes from the Pacific Coast of North America. If the species is correctly assigned, it would be one of the earliest known records for this genus.

Two additional hand specimens from LACMIP loc. 16869 also contain aligned teredinid tubes, but none shows the concamerations of the tubes shown in Figure 14. They might represent another, unidentified (genus and) species of teredinid, or they might be tubes of juvenile animals that had yet to develop the concamerations. They might also simply represent differences in preservation. The shell material of the tubes on the additional hand specimens is still present.

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APPENDIX

LOCALITIES CITED

WASHINGTON

CSUN 1563. At elevation of 680 m (2230 ft.), roadcut exposure on NE side of logging road, 300 m N and 50 m E of SW corner of section 1, T. 17 N, R. 4 W, WBM, and 500 m S32°E of Larch Mountain, U. S. Geological Survey 7.5-minute Capitol Peak, Washington quadrangle,

1986 edition (provisional), Thurston County, Washington. Crescent Formation. Age: Middle early Eocene ("Capay Stage"). Collectors: J. L. Goedert & G. H. Goedert, July, 1992. [= LACMIP loc. 16655].

CALIFORNIA

The following information is applicable to the following localities: U. S. Geological Survey, 7.5-minute Topanga, California quadrangle, 1952 (photorevised 1981) edition, Palisades Highlands and vicinity, east–central Santa Monica Mountains, Los Angeles County, southern California. Upper part of the Santa Susana Formation. Age: Late Paleocene (Thanetian Stage).

LACMIP loc. 11984. Locality now covered by a homesite in a housing tract called "The Summit"; just below algal limestone at an elevation of about 419 m (1375 ft.), about 488 m (1600 ft.) S50°W of hill 1672, slightly E of the SE edge of the first "e" in the word "FIRE-BREAK," on a ridge between forks of upper Pulga Canyon. City of Los Angeles. Collector: J. M. Alderson, 1988.

LACMIP loc. 16869. Locality now covered by 2 to 3 m of fill underlying a homesite in a gate-guarded housing tract called "The Enclave," which is part of the community of Palisades Highlands; at the west end of Calle Bellevista at 16865 Calle Bellevista; approximately 20 m below algal limestone at elevation 450 m (1475 ft.), on the east side of Trailer Canyon, which is a tributary to Santa Ynez Canyon, in an unsurveyed area 5.6 km (3.47 mi.) E and 1.15 km (0.71 mi.) S of the SW corner of section 7, T. 1 S, R. 16 W, SBBM. City of Los Angeles. Collector: W. L. Rader, 1992. [= CSUN loc. 1590].

LACMIP loc. 16888. Locality now covered by 2 to 3 m of fill underlying homesites in a gate-guarded housing tract called "The Enclave," which is part of the community of Palisades Highlands; along the south side of Calle Bellevista; just above algal limestone and about 20 m (estimated) stratigraphically above LACMIP loc. 16869. City of Los Angeles. Collector: W. L. Rader, 1992.

LACMIP loc. 16897. In unweathered bluish gray siltstone above the "B" in southernmost word "FIRE-BREAK," 290 m (950 ft.) S and 335 m (1100 ft.) W of hill 1672 along E side of upper Pulga Canyon. Locality is about 100 m NW of corner of Chastian Parkway and Calle Jermaine in the Summit housing tract of Palisades Highlands. City of Los Angeles. Locality is now covered by homesites. Collectors: W. L. Rader & R. L. Squires, June 16, 1996.

LACMIP loc. 26814. Just below algal limestone, 853 m (2800 ft.) W of hill 2036, bottom of south-flowing tributary of Quarry Canyon, latitude 34°05′24″N, longitude 118°33′30″W. Collector: J. M. Alderson, January, 1981.

THE VELIGER

The Veliger 41(2):172–179 (April 1, 1998)

Investigation of the Influence of Exposure to Predation Risk on the Development of Defensive Behaviors in a Marine Gastropod

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Abstract. We examined the hypothesis that defensive behavioral responses of the whelk *Buccinum undatum* to its predator, the asteroid *Leptasterias polaris*, develop with experience with predation risk in the environment. Small whelks (2–3 and 4–5 cm in length) did not show an increase in responsiveness after conditioning for 2 mo to odors of *L. polaris* feeding on whelks and repeated predatory attacks. Our results suggest either (1) that the responsiveness of whelks to *L. polaris* is not related to exposure to predation risk or (2) that our experiment did not adequately replicate natural conditions that lead to a development of the whelk's escape response. A decrease in responsiveness to the predator (and a tendency toward decreased growth) with increasing levels of predation risk during the conditioning period suggests that the intensity and duration of exposure to the predator were too great. Studies are required to evaluate whether escape responses develop using less frequent and shorter contacts with the predator.

INTRODUCTION

Numerous studies show that predators can induce changes in the morphology or behavior of their prey over ecological time scales. For example, the development of morphological defenses following exposure to predators has been documented in bryozoans (Yoshioka, 1982; Harvell, 1984), bivalves (Reimer & Tedengren, 1996), crustaceans (Lively, 1986) and fishes (Fuiman, 1993; Brönmark & Petterson, 1994) and the development of behavioral defenses in protozoans (Kusch, 1993), insects (Craig, 1994), amphibians (Semlitsch & Reyer, 1992; Suboski, 1992), reptiles (Suboski, 1992), fishes (Csányi, 1985; Magurran, 1990; Fuiman, 1993; Chivers & Smith, 1994), birds (Conover, 1987; Maloney & McLean, 1995), and mammals (Williams et al., 1990). Such phenotypic changes are considered adaptations to reduce predation risk, which is defined as the probability of mortality from predation over a given time interval (Lima & Dill, 1990).

In gastropods, many studies show that the presence of predators can induce morphological changes, such as increased shell thickness or the production of spines (Newkirk & Doyle, 1975; Vermeij, 1982; Appleton & Palmer, 1988; Palmer, 1990), or changes in life-history strategies (Crowl & Covich, 1990; Rawlings, 1994). However, no studies have investigated the development of defensive behaviors in response to predators. This is surprising given the spectacular and well-documented escape behaviors described for many gastropods, particularly in response to predatory asteroids (e.g., Feder, 1963; Ansell, 1969; Phillips, 1976, 1977, 1978; Miller, 1986).

Striking escape responses are particularly well documented in the common whelk *Buccinum undatum* L. in the northern Gulf of St. Lawrence, eastern Canada, in response to its major predator in the region, the asteroid *Leptasterias polaris* (Müller & Troshel). Contact with and chemical cues (saponins) from *L. polaris* induce defensive behaviors in the whelk (Harvey et al., 1987; Legault & Himmelman, 1993; Rochette et al., 1996), such as increased locomotion, rocking of the shell from side to side, and, if the stimulus is sufficiently intense, rapid extension and twisting of the foot (foot contortions). These types of behaviors are also exhibited by European *B. undatum* in response to the predatory asteroid *Marthasterias glacialis* (Feder, 1967). The development of reliable defense behaviors in *B. undatum* in the northern Gulf is likely advantageous because it decreases vulnerability so that the whelk can approach feeding seastars to profit from feeding opportunities (Rochette et al., 1995).

Interestingly, Rochette et al. (1996) show that not all *B. undatum* are responsive to *L. polaris*. Whelks from the Bay of Fundy, which are allopatric with *L. polaris*, exhibit only slight responses to contact with and odors from *L. polaris*. Also, newly emerged naive whelks, both from regions where whelks are sympatric and allopatric with *L. polaris*, do not exhibit violent foot contortions. Finally, in the northern Gulf of St. Lawrence, responsiveness of whelks toward *L. polaris* increases with whelk size (Rochette et al., 1996), which may account for the decrease in whelk vulnerability to *L. polaris* with increasing size (Rochette & Himmelman, 1996). The above observations suggest that escape behaviors of *B. undatum* develop in response to detection of predatory risk in the environment. The present study experimentally examines whether the responsiveness of the whelk to *L. polaris* increases in response to detection of predation risk. We

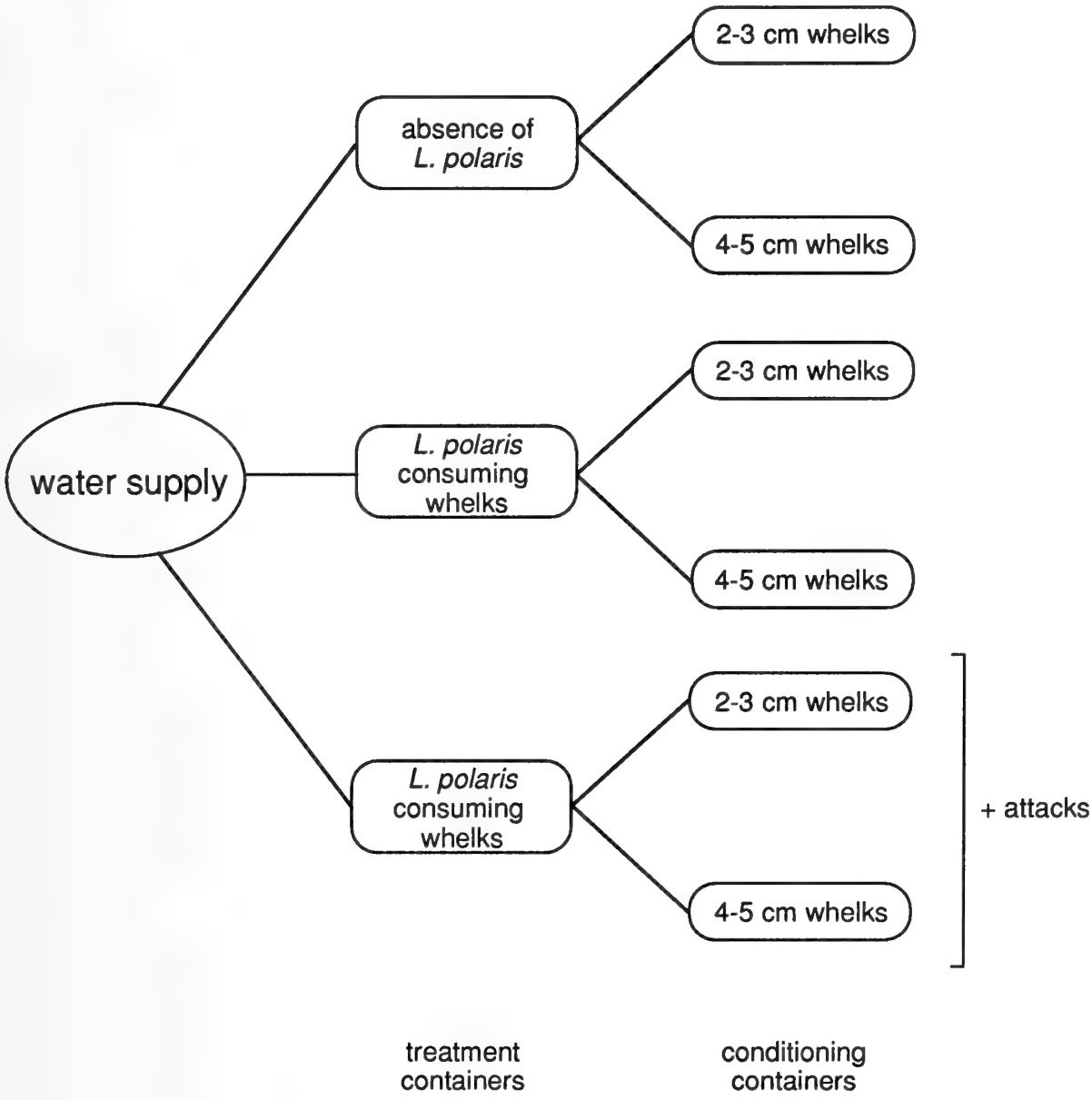

Figure 1

Schematic representation of the experimental set-up in which two sizes of whelks *Buccinum undatum* (2–3 and 4–5 cm in shell length) were maintained for 2 mo in 25-L conditioning containers. The whelks were subjected to three treatments: (1) supplied with water which flowed through a 25-L container containing no predator, (2) supplied with water which flowed through a 25-L container in which *Leptasterias polaris* was consuming whelks, and (3) subjected to periodic attacks by *L. polaris* in addition to being supplied with water scented with the predator consuming whelks. The three predator treatments were replicated four times for each size group.

evaluate this hypothesis by exposing whelks to two stimuli: (1) to odors of *L. polaris* feeding on whelks and (2) to odors of *L. polaris* feeding on whelks plus periodic attacks on the experimental whelks by *L. polaris*. We considered that these stimuli would represent strong and very strong predatory risk, respectively.

MATERIALS AND METHODS

Our experiments were conducted from June through August 1995 in a wet laboratory at Havre-St.-Pierre (50°14′N, 63°35′W), northern Gulf of St. Lawrence. The laboratory was supplied with running seawater (4 to

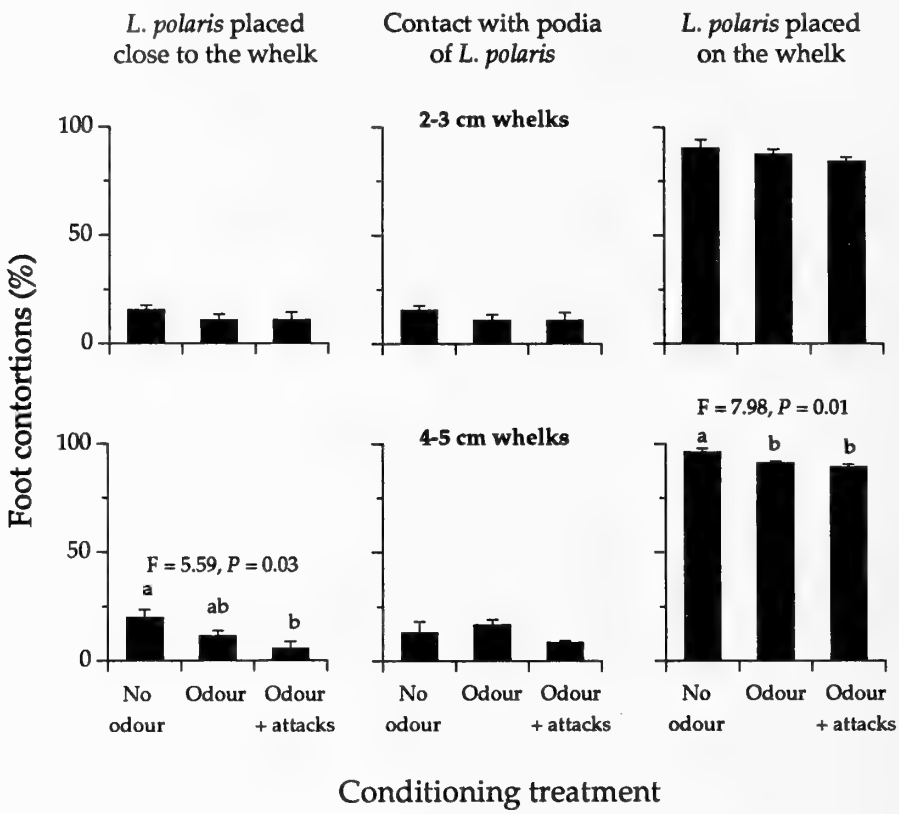

Figure 2

Percentage of whelks, *Buccinum undatum*, showing foot contortions in tests with three stimuli: (1) a *Leptasterias polaris* being held for 2 min at a distance of half the shell length of the whelk from the anterior end of the whelk, (2) a 1-s contact with the terminal podia of one arm of *L. polaris* (after this, the asteroid was left at a distance of half the shell length of the whelk), and (3) a contact with the mouth region of *L. polaris* (the asteroid was placed on the whelk), after the 2-mo of conditioning to three levels of predation risk (see Figure 1). Vertical bars represent the standard errors. For each size group of whelks and each stimulus, data for the three conditioning treatments were compared using an ANOVA. Where differences were detected, we followed with two-by-two comparisons using Tukey-Kramer tests (bars not sharing the same letters were different, $P < 0.05$).

11°C) pumped from 10 m in depth. The whelks were collected at Cap du Corbeau, near Havre-St-Pierre, where they occur sympatrically with the predatory asteroid *L. polaris*. Whelks were acclimatized to laboratory conditions for 2 wk before the beginning of the experiment in 100-L tanks continuously supplied with seawater (predators and food absent). The predators used in the conditioning treatments were *L. polaris* measuring 25–35 cm in diameter which had also been collected at Cap du Corbeau.

As the responsiveness of whelks has been shown to increase with size (Rochette et al., 1996), we performed experiments on two groups of small whelks, measuring 2–3 and 4–5 cm in shell length, respectively. Each was conditioned for 2 mo under three treatments (Figure 1) which represented a gradient in predation risk: (1) absence of predator (and absence of dead whelks), (2) presence of odors from a predator consuming 2–4 cm whelks, (3) presence of odors from a predator consuming 2–4 cm whelks combined with periodic attacks on the whelks by the predator. Previous studies of morphological changes in gastropods in response to the presence of predators used conditioning periods of > 3 mo (Appleton & Palmer, 1988; Palmer, 1990). As we expected that behavioral response would develop more rapidly, we chose a conditioning period of 2 mo.

For each of the two sizes of whelks and three conditioning treatments we maintained four groups of 28 whelks, each in a 25-L container supplied with running seawater (1 to 1.5 L.min-1) coming from a 25-L treatment container (Figure 1). For the first conditioning treatment (absence of predator), the container supplying water contained no predator or whelks. In the predator-odor treatments, an asteroid consuming a whelk was maintained in treatment containers for the first 4 sequential days per 8-d cycle. In the third treatment condition, in addition to

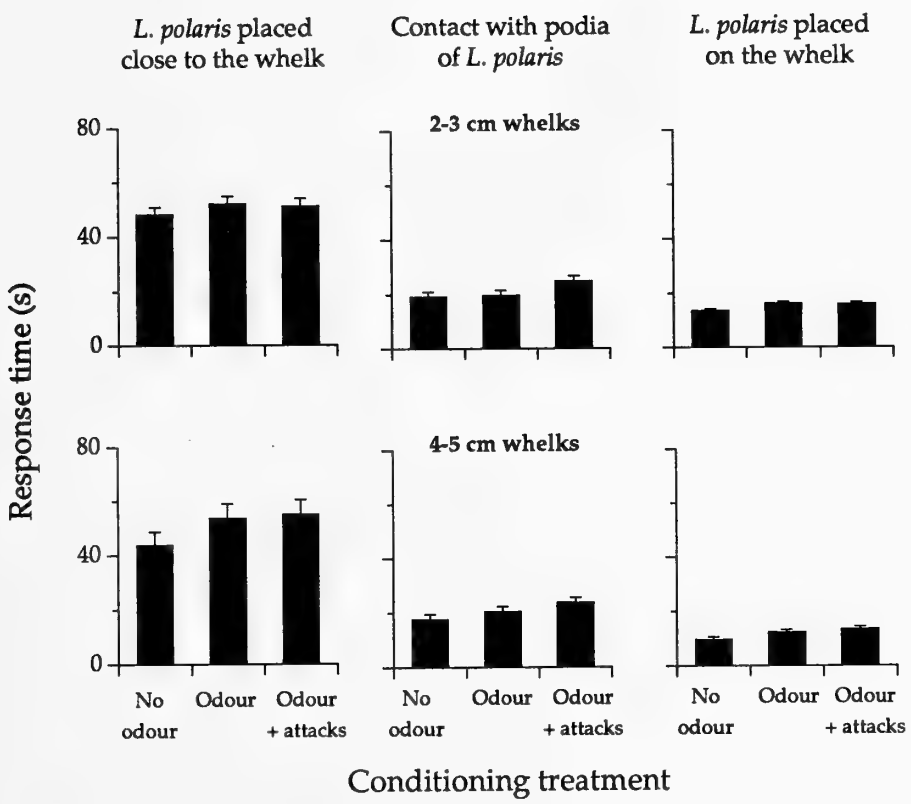

Figure 3

Response time of whelks in tests with three stimuli: (1) a *Leptasterias polaris* being held for 2 min at a distance of half the shell length of the whelk from the anterior end of the whelk, (2) a 1-s contact with the terminal podia of one arm of *L. polaris* (after this, the asteroid was left at a distance of half the shell length of the whelk), and (3) a contact with the mouth region of *L. polaris* (the asteroid was placed on the whelk), after the 2 mo of conditioning to three levels of predation risk (see Figure 1). For each size group of whelks and each stimulus, data for the three conditioning treatments were compared using a nested ANOVA.

the odors of *L. polaris* consuming conspecifics, whelks were individually subjected to simulated predator attacks on the fifth or sixth day of each 8-d cycle. In these attacks, we first touched the siphon of the whelk with the podia of *L. polaris* and then placed an arm of *L. polaris* on the whelk. The diameter of *L. polaris* used in the attacks was about 3 times the length of the whelk. Whelks in all three conditioning treatments were supplied with food (herring, scallop viscera, or mussels) on the second and third day of each 8-d cycle, and at the end of the third day, the tanks were cleaned and remaining food removed. The positions of treatment containers in the laboratory, each supplying water to two experimental groups of whelks (Figure 1), were determined at random.

At the end of the 2-mo conditioning period, we quantified the escape response of all the whelks. We first recorded the responses of each whelk to three increasing levels of predation threat: (1) a *L. polaris* held for 2 min in front of the whelk, at a distance of half its shell length, (2) a 1-s contact with the terminal podia on one arm of *L. polaris* (after this, the asteroid was left at a distance of half the shell length of the whelk), and (3) the mouth region of *L. polaris* being placed on the whelk. At each step, observations of the behavior of the whelks were made for 2 min. In these tests, the diameter of the *L. polaris* was about 3 times the length of the whelk being tested, and the asteroid used was randomly selected from 35 individuals for each size group. The above tests were conducted in 10-L containers (25 × 40 × 10 cm) with a sand bottom, and after each test the containers were cleaned and the sand changed. We noted the response time and the type of defensive behavior in two categories of increasing intensity, shell rocking (twisting of the shell by $> 90°$ in respect to the direction of the foot) and foot contortions.

Two weeks later, we also evaluated the response of whelks to concentrated odors of *L. polaris*, by placing each whelk in water taken from a 6.5 L receptacle which had contained one 25–35 cm *L. polaris* for 1 h. We observed each whelk for 2 min and noted the behavior exhibited and associated response time.

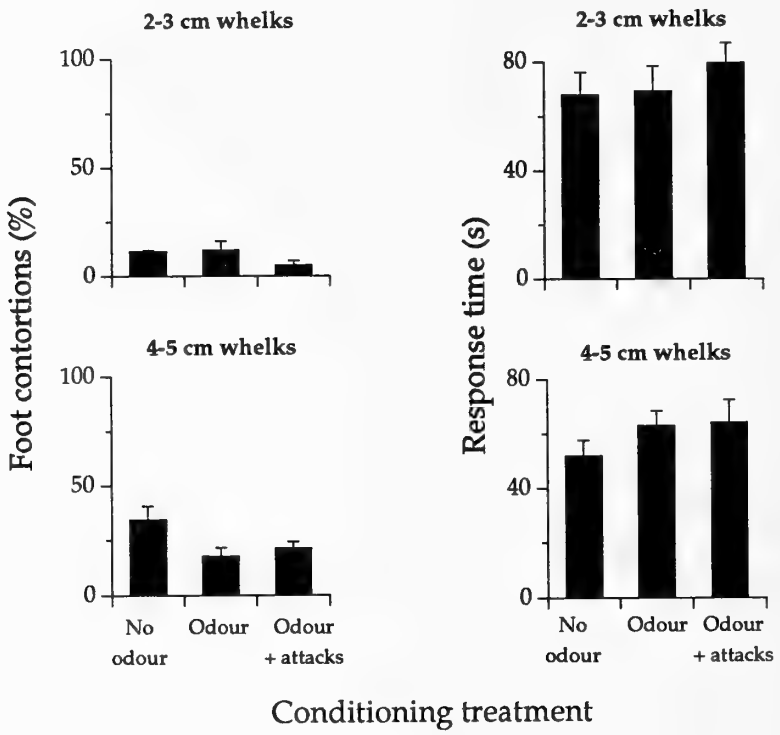

Figure 4

Percentage of individuals showing foot contortions and response time for whelks, *Buccinum undatum*, conditioned during 2 mo to three levels of predation risk (see Figure 1) when tested with concentrated odors of *L. polaris*. Vertical bars represent the standard errors. Foot contortion responses were compared as in Figure 2 and response times as in Figure 3.

All statistical comparisons of behavioral responses of whelks were applied separately for each of the two sizes of whelk and for each of the four test conditions: (1) *L. polaris* placed close to the whelk, (2) contact with the podia of *L. polaris*, (3) *L. polaris* placed on the whelk, and (4) exposure to concentrated odors of *L. polaris*. In the tests comparing the proportions of whelks showing any given type of response (shell rocking or foot contortions), the data were first arcsin transformed so that assumptions of normality (Shapiro-Wilks, $P > 0.05$) and homoscedasticity (Levene, $P > 0.05$) were respected. Then we applied ANOVAs to compare the whelks conditioned for 2 mo to the three levels of predation risk (no odor, odor, odor plus attacks). When significant differences among conditioning treatments were detected, we followed with Tukey-Kramer multiple comparisons tests. We further used nested ANOVAs to compare response times for any given behavior for the whelks from the three 2-mo conditioning treatments (four samples of about 28 whelks per treatment). All data respected assumptions of normality and homoscedasticity.

Finally, we measured the shell length of the whelks at the beginning and end of the 2-mo experimental period and used ANOVAs to compare growth rates among the three conditioning treatments. As whelks were not individually marked, we calculated growth rate from the average increments per experimental groups (four groups per treatment).

RESULTS

The experiments did not provide evidence that responsiveness increased with exposure to predation risk during the conditioning period. For example, the tests at each of the three levels of predation threat (predator nearby, contact with the predator, and attack by the predator) performed on each of the two size groups of whelks studied did not indicate that the proportion of individuals showing foot contortions (the strongest defensive response) increased with increasing exposure to *L. polaris* during the conditioning period (Figure 2). In fact, the opposite trend was observed in two instances for 4–5 cm whelks (Figure 2). Similarly, we did not detect increases in the proportion of whelks showing shell rocking with increasing predation threat during the conditioning period (ANOVAs, $P > 0.05$; data not shown). Also, the response time for the strongest response (Figure 3), and also for any particular response (data not shown), did not decrease with increas-

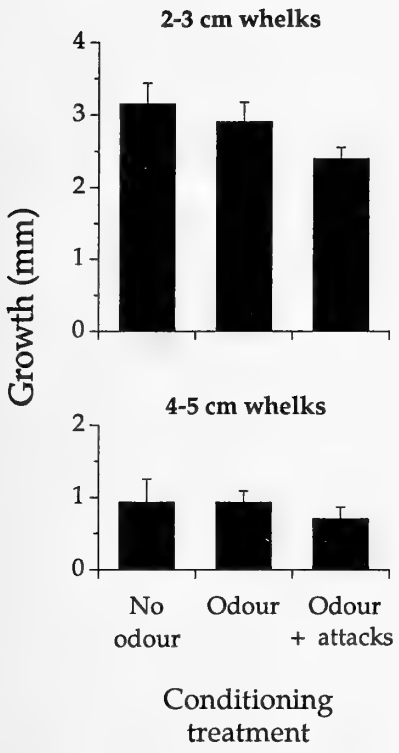

Figure 5

Growth of three groups of whelks during 2 mo of conditioning to three levels of predation risk (see Figure 1). Vertical bars represent the standard errors. For each size group of whelk, data for the three conditioning treatments were analyzed using an ANOVA, and no significant differences were detected.

ing exposure to *L. polaris* during the conditioning period, and in most cases the opposite trend was suggested.

The data on the responses of whelks exposed to water which had been strongly scented by odors of *L. polaris* similarly did not support the hypothesis that escape responses increase with increasing exposure to predation threat. For each of the two size groups of whelks, no significant differences were found among whelks maintained for 2 mo under the three different levels of predation risk, either in the proportion of individuals showing foot contortions or in their response time (Figure 4, ANOVAs, $P > 0.05$). This result was also obtained when the data on the proportion of individuals showing shell rocking were analyzed (ANOVAs, $P > 0.05$).

Growth of Whelks Maintained under Different Levels of Predation Risk

For both 2–3 cm and 4–5 cm whelks, mean growth rates decreased progressively for individuals conditioned in the three increasing levels of predation risk (Figure 5). However, these trends were not significant ($P = 0.15$ for 2–3 cm whelks, $P = 0.74$ for 4–5 cm whelks).

DISCUSSION

Our study on small whelks, for which escape responses are not well developed, conditioned for 2 mo to odors of *L. polaris* feeding on conspecifics and simulated predatory attacks, showed no evidence of an increase in responsiveness resulting from exposure to the predator. Rather, our results suggest either (1) that the responsiveness of whelks to *L. polaris* is not related to prior exposure to predation risk or (2) that our experiment did not adequately replicate natural conditions that lead to a development of the whelk's escape response. Although we cannot refute the first hypothesis, the tendency toward reduced growth and the evidence for reduced responsiveness of experimental whelks suggest that whelks were overly exposed to predation-related chemicals during the experiment. A decrease in whelk condition in our study may have been related to the toxicity of steroid glycosides (saponins) which are produced by asteroids (Lucas et al., 1979; Iorizzi et al., 1995). A waning of escape responses after prolonged contact with asteroids has also been reported for the limpet *Diodora aspera* (Margolin, 1964).

It is unlikely that the decrease in responsiveness of conditioned whelks was due to muscular fatigue because the whelks had not been stimulated to react to asteroids during the 2 wk prior to the odor tests. It is more likely that excessive exposure to chemicals from predators and dead conspecifics affected the whelks' nervous system, causing either habituation or sensory adaptation. Both phenomena involve the waning of a response following excessive exposure to a given stimulus, but only habituation is specific to a single stimulus. We cannot evaluate these two possibilities because we did not examine the response of whelks to other chemical cues (Thompson & Spencer, 1966).

Our study is the first to examine if anti-predator behaviors of gastropods develop following experience with predation risk in the environment. We found no evidence of learning in *B. undatum* following exposure to predation risk. Nevertheless, several studies demonstrate that the behavioral patterns exhibited by gastropods can be modified through experience (*Aplysia* spp.: Carew & Kupfermann, 1974; Walters et al., 1981; *Helix* spp.: Balaban, 1987; Balaban & Bravarenko, 1993; *Hermissenda* spp.: Alkon, 1980; Grover et al., 1987). For example, the nudibranch *Aplysia californica* develops a gill-withdrawal reflex following tactile stimulation (Kandel & Schwartz, 1982.). The increased responsiveness in *A. californica* is very rapid, requiring from several hours to as little as a few minutes; however, if the stimulation is applied repetitively, the response eventually decreases. Most studies demonstrating behavioral developments in gastropods involve much shorter exposure to the conditioning stimuli than that required for the development of morphological changes. Although our general experimental design involved a 2-mo conditioning period, behavioral responses

to the simulated attacks were determined on the eighth day and at 8-d intervals thereafter. Whereas these data did not show significant variations over time ($P \geq 0.05$, ANOVA), it is possible there was a change during the first 8 d and then no change or a slight decrease thereafter. We are presently planning experiments to test whether ecsape behaviors develop in response to less frequent and shorter contacts with the predator.

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THE VELIGER

Spawning of the Iceland Scallop (*Chlamys islandica* Müller, 1776) in the Northern Gulf of St. Lawrence and Its Relationship to Temperature and Phytoplankton Abundance

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Abstract. We determined the spawning period for the Iceland scallop, *Chlamys islandica*, over 3 yr in the Mingan Islands, northern Gulf of St. Lawrence. Sharp drops in gonadal mass indicated that spawning began in late July in 1990 and 1991, whereas it was not initiated until mid-August in 1995. No consistent relationship between temperature and spawning was evident: spawning occurred during a temperature increase in 1991 and during low and weakly fluctuating temperatures in 1990 and 1995. Further, spawning did not appear to be related to day length or a particular lunar phase, and salinity fluctuations were likely too slight to have acted as a spawning cue. All three observed spawnings coincided with increases in chlorophyll *a* levels which indicates that *C. islandica* spawning may be triggered by summer phytoplankton blooms.

INTRODUCTION

Reproduction in marine invertebrates is generally controlled by a combination of endogeneous factors (neurosecretion) and exogeneous factors, such as temperature, food availability, and photoperiod (Giese & Kanatani, 1987). This allows the coordination of gonadal maturity among individuals within populations. For species with external fertilization, the release of gametes into the environment is a critical event because its timing may strongly influence fertilization success and the growth and survival of larval stages (Thorson, 1950; Himmelman, 1981). Since gametes are usually viable for a short period of time and a high concentration is required to ensure encounters between eggs and sperm (Pennington, 1985), fertilization success may depend on the degree of synchrony of spawning individuals. Once reproductive maturity is reached, spawning synchrony within a population is generally achieved by responding to changes in a particular environmental factor such as temperature, salinity, photoperiod, or phytoplankton abundance (Himmelman, 1981; Giese & Kanatani, 1987; Starr et al., 1990).

Knowledge of reproduction is essential to the understanding of recruitment processes and for effective management of commercially exploited species. The Iceland scallop, *Chlamys islandica* (O. F. Müller, 1776), is a subarctic species which is found along the coasts of the North Atlantic and Arctic oceans (Ekman, 1953). Over the past 20 yr, the commercial exploitation of Iceland scallops has expanded greatly in eastern Canada. Scallop landings (mostly *Placopecten magellanicus*) in the Magdalen Islands and Gaspé Peninsula have plummeted since the 1980s and have not yet recovered (Giguère & Miller, 1993). In contrast, Iceland scallop landings in the Mingan Islands, northern Gulf of St. Lawrence, have increased since the 1980s so that this region now supports the most important scallop fishery in Québec (Giguère & Miller, 1993). In spite of the commercial and economic importance of *C. islandica* in eastern Canada, little is known about its reproduction. Studies on *C. islandica* reproduction are mostly limited to northeastern North Atlantic populations (Skreslet & Brun, 1969; Skreslet, 1973; Sundet & Vahl, 1981; Sundet & Lee, 1984; Thorarinsdòttir, 1993). The only report of its reproduction in Canadian waters is for a population of the Magdalen Islands (Giguère et al., 1994).

The objective of the present study was to determine the spawning period of the Iceland scallop in the Mingan Islands, northern Gulf of St. Lawrence, and to examine its relationship to environmental factors.

MATERIALS AND METHODS

The population studied was located at Île du Fantôme in the Mingan Islands, northern Gulf of St. Lawrence, eastern Canada (50°13′6″N, 63°41′12″W). Samples of 30–40 sexually mature *Chlamys islandica* (75–100 mm in shell height) were collected by SCUBA divers periodically from June through August at 37 m in depth in 1990, and at 24 m in 1991 and 1995. Within 2 h of collecting the scallops, we determined shell height and the wet mass (after draining for 10 min on paper towelling) of the gonad and remaining soft tissues. Seasonal changes in gonadal mass were analyzed using analysis of covariance (ANCOVA) with shell height as covariate to adjust gonadal mass for variations in shell height (Huitema, 1980).

A gonadal index was not used because the effect of scallop size was not entirely corrected for when gonadal mass was divided by either muscle mass or viscera mass (Bonardelli & Himmelman, 1995). The ANCOVAs standardized the gonadal mass of scallops to mean shell height (86.6 ± 0.2 mm in 1990, 88.3 ± 0.2 mm in 1991, and 87.2 ± 0.3 mm in 1995, $\bar{x}$ ± SE). As seasonal changes in gonadal mass did not vary between males and females ($P > 0.40$), sexes were pooled for analysis. Gonadal mass and shell height values were log transformed prior to the analyses. When ANCOVAs indicated significant differences among sampling dates, we followed with comparisons of adjusted gonadal masses between dates using Bryant-Paulson-Tukey multiple comparisons tests (Huitema, 1980).

Temperature on the scallop bed was recorded using a Peabody-Ryan thermograph in 1990, a Sealog-T thermograph (Vemco, Inc.) in 1991, and an Aanderaa RCM4S current meter in 1995. These instruments were anchored to the bottom. From these measurements, we calculated daily mean temperature and daily temperature variance divided by daily mean temperature as a measure of temperature variability. Further, we calculated cumulative day degrees from when the instruments were placed in the field to the onset of spawning. Phytoplankton abundance was determined periodically from water samples collected within 1 m of the scallop bed using Niskin sampling bottles. From each sample, chlorophyll *a* determinations (corrected for phaeopigment content) were made using the spectrophotometric or fluorimetric methods as described by Parsons et al. (1984). To assess spatial variability in our estimates of phytoplankton abundance, we collected replicate samples in 1995. Because of logistic limitations, the latter were frozen at −20°C for 1 mo prior to determination of chlorophyll *a* concentration. Consequently, chlorophyll *a* values for 1995 were likely underestimated because of the deterioration of photosynthetic pigments during the 1 mo delay between sampling and the determination of pigment levels (Parsons et al., 1984). Finally, daily tidal amplitude was calculated from tables published by the Canadian Hydrographic Service.

RESULTS

Gonadal mass varied in a remarkably similar pattern in 1990 and 1991 (Figure 1), showing a slight and nonsignificant ($P > 0.05$) increase from early June to late July followed by a drop ($P < 0.05$) between 18 and 26 July in 1990, and between 23 and 27 July in 1991 (Figure 1). Thereafter, gonadal mass gradually decreased until 26 August 1990 and 1991. In contrast, in 1995, gonadal mass increased slightly ($P > 0.05$) from early June to early August and dropped abruptly between 8 and 14 August (Figure 1). Thus, abrupt decreases in gonadal mass occurred in late July in 1990 and 1991 and in mid August in 1995.

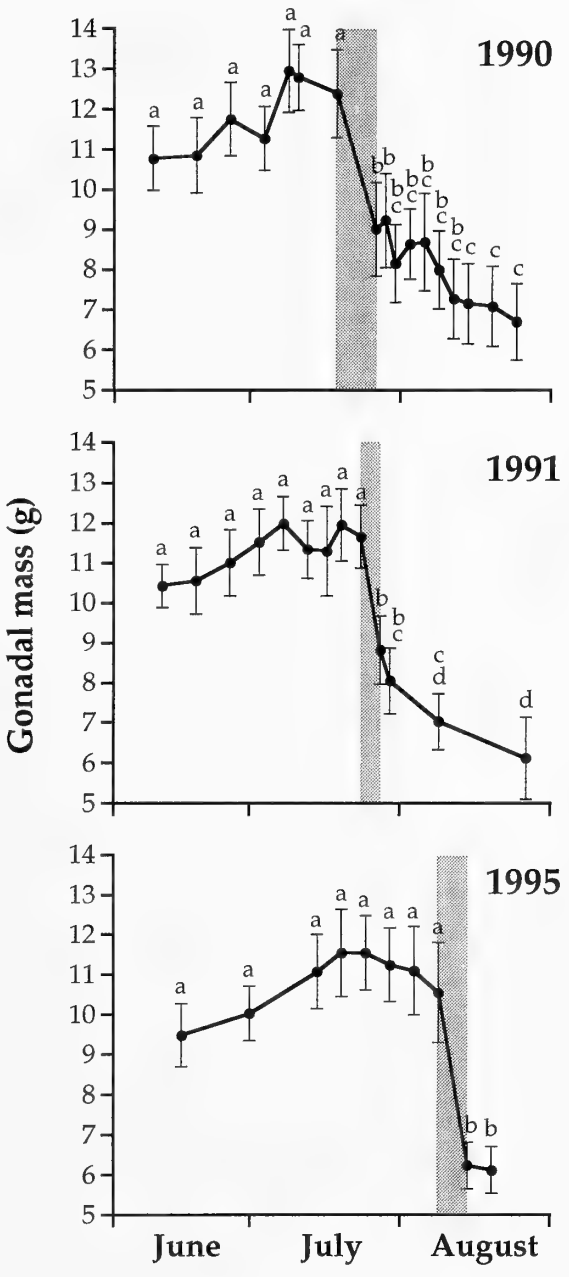

Figure 1

Seasonal changes in gonadal mass of the Iceland scallop, *Chlamys islandica*, at Île du Fantôme, Mingan Islands, in the northern Gulf of St. Lawrence, during the summers of 1990, 1991, and 1995. Gonadal masses ($\bar{x}$ ± SE) are adjusted for variations in shell height using ANCOVAs (see Materials and Methods). Samples sharing the same letters are not significantly different ($P > 0.05$) as determined by Bryant-Paulson-Tukey multiple comparisons. Shaded areas delimit spawning periods.

Seasonal changes in temperature conditions varied markedly among the 3 years of our study (Figure 2). During late June 1990, mean daily temperature increased from 3.6 to 7.4°C and then fell to < 3.5°C. Temperatures remained low (< 4.0°C) until 29 July, when a second sharp increase began (3.9 to 6.9°C in 4 d). Daily temperature variability (variance/mean) followed a similar pattern, there being a general increase from late June to early July, low values (< 0.05) until 29 July, and then a sharp increase (0.05 to 0.11). Thus, the abrupt decrease in gonadal mass between 18 and 26 July 1990 occurred within the period of low and weakly fluctuating temperatures (3.0 to 4.7°C). Mean daily temperature in 1991 and 1995, where we studied spawning at a shallower depth (24 rather than 37 m), showed bimonthly increases of 2–4°C which corresponded to periods of spring tides (Figure 2). Further, daily temperature variability was generally higher and exceeded 0.1 throughout most of July. The abrupt decrease in gonadal mass between 23 and 27 July 1991 coincided with increases in daily mean temperature (from 2.5 to 5.1°C) and in temperature variability (from 0.12 to 0.30), whereas the decrease between 8 and 14 August 1995 coincided with low (< 4.2°C) and weakly fluctuating temperatures (0.05 to 0.10). Finally, cumulative day degrees at the onset of the sharp gonadal decrease varied markedly among the 3 years in our study: 156°C in 1990, 139°C in 1991, and 189°C in 1995.

The sharp decreases in gonadal mass in all 3 years coincided with increases in phytoplankton abundance (Figure 2). In 1990, chlorophyll *a* levels varied between 0.50 and 0.85 $\mu g \cdot L^{-1}$ until early July and then increased from 0.63 to 1.59 $\mu g \cdot L^{-1}$ between 9 and 26 July. In 1991, chlorophyll *a* values were below 0.87 $\mu g \cdot L^{-1}$ until mid July, and increased from 0.47 to 1.32 $\mu g \cdot L^{-1}$ between 17 and 27 July. In 1995, chlorophyll *a* values were below 0.48 $\mu g \cdot L^{-1}$ until a sharp increase from 0.35 to 0.94 $\mu g \cdot L^{-1}$ was recorded between 8 and 9 August. Our replicate samples in 1995 (Figure 2) indicated low spatial variability in phytoplankton abundance (coefficient of variation < 15%) and this was likely because of the high turbulence at our study site.

In all 3 years, sharp drops in gonadal mass occurred during a period of spring tides (Figure 2). However, the tidal amplitude varied between years. In 1990 and 1995, the maximum amplitude was ≈ 30% greater than in 1991 (Figure 2). Finally, the abrupt decreases in gonadal mass in 1990 and 1995 occurred during new moon phases, whereas the decrease in 1991 occurred just prior to a full moon (Figure 2).

DISCUSSION

Although we did not use histology to assess the state of the gonad, many studies demonstrate that sharp drops in gonadal mass in *Chlamys islandica* (Sundet & Lee, 1984; Thorarinsdòttir, 1993) and other scallops (Beninger, 1987; Barber & Blake, 1991; Schmitzer et al., 1991; Dibacco et al., 1995) are due to spawning. It may be argued that decreases in gonadal mass could also result from the lysis and resorption of gametes; however, these processes cause only slight and slow changes in gonadal mass in scallops as they usually involve a small proportion of gametes (Schmitzer et al., 1991; Dibacco et al., 1995). Because of this, the abrupt decreases in gonadal mass in our study were most likely due to spawning.

The precipitous drops in gonadal mass indicated that spawning of *Chlamys islandica* in the Mingan Islands occurred in late July in 1990 and 1991 and in mid August in 1995. Similar abrupt spawnings have been reported for Iceland scallops in Norway and Iceland, although several weeks earlier, late June to early July (Skreslet & Brun, 1969; Skreslet, 1973; Thorarinsdòttir, 1993). Such strongly synchronized events within populations suggest coordination by environmental cues.

Temperature, either attaining a certain level or a critical change, has more than any factor been suggested to control spawning in marine invertebrates (Giese & Kanatani, 1987). For several scallop species, correlative studies have suggested that fluctuations in temperature, related to wind, tides, or downwelling events, act as the natural spawning cue (Sastry & Blake, 1971; Broom & Mason, 1978; Miller et al., 1981; Bonardelli et al., 1996). Our study, which involved continuous recording of temperature and frequent sampling of scallops, did not indicate a consistent relationship between temperature and spawning in *C. islandica*. Although spawning in 1991 coincided with increases in mean temperature and in temperature variability, spawnings in 1990 and 1995 occurred during periods of low and weakly fluctuating temperatures. In all 3 years, no spawning occurred during marked temperature increases several weeks prior to spawning. Although this might be attributed to a lack of gonadal maturity, we consider this unlikely. Gonadal size had peaked more than a month prior to the delayed spawning in 1995. In the 3 years of our study, markedly warmer periods followed spawning, but could not be considered as spawning cues. Finally, the onset of spawning did not appear to be related to a critical cumulative temperature. Although our temperature records began 2 wk later in 1995, cumulative day degrees at the onset of spawning were markedly higher than in 1990 and 1991 (33°C and 50°C higher, respectively).

In all but one of the previous studies of *C. islandica* spawning, temperature was the only environmental factor studied. Data reported by Giguère et al. (1994) showed an increase in mean temperature from 10 to 13°C during spawning in the Magdalen Islands, eastern Canada. Skreslet & Brun (1969) and Skreslet (1973) suggest that temperature variations act as the spawning cue for *C. islandica* in Norway. Skreslet & Brun (1969) attributed July spawnings in Balsfjord to tidally induced oscillations of the thermocline over the scallop bed. However, the

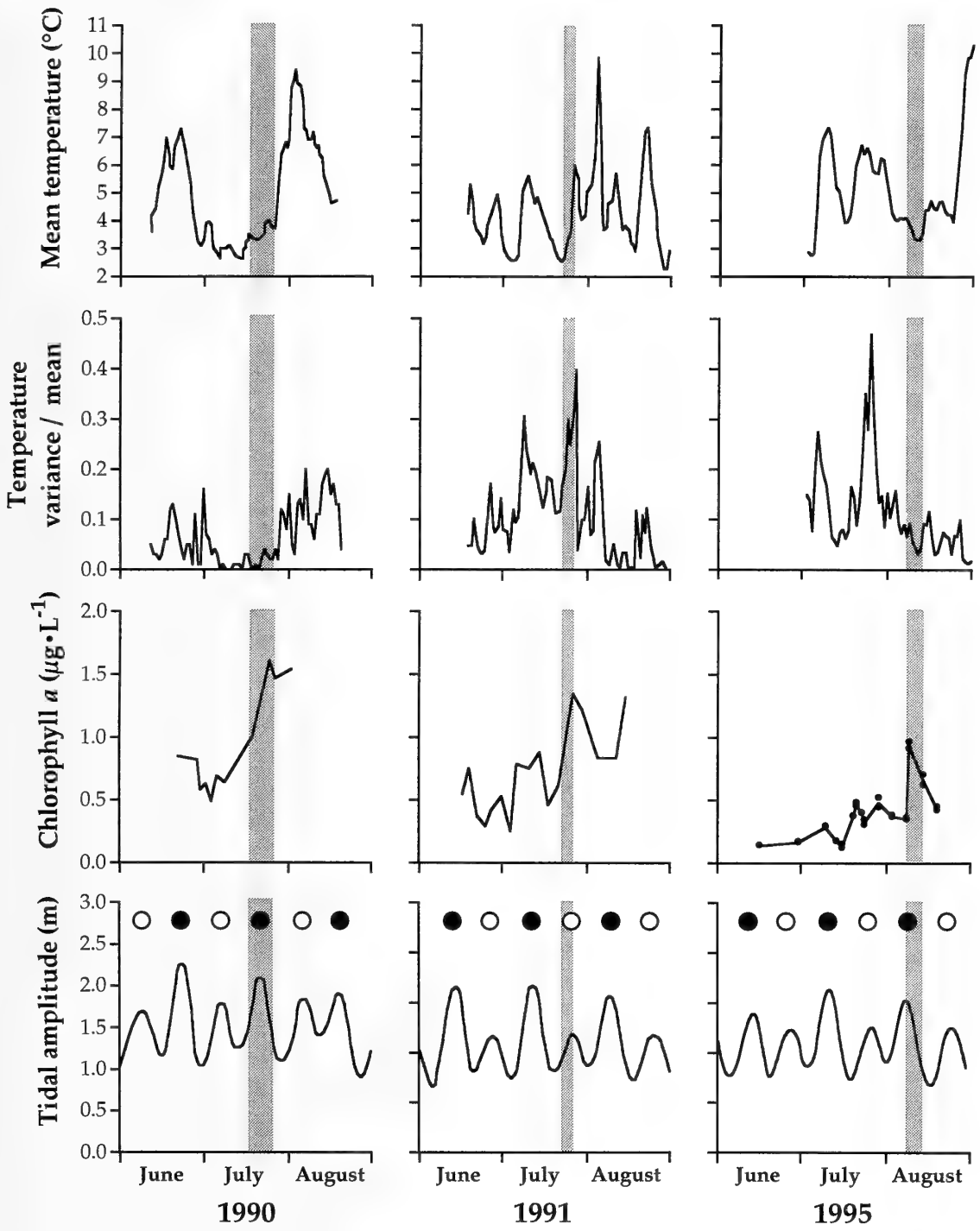

Figure 2

Seasonal variations in environmental factors during the summers of 1990, 1991, and 1995 over the Iceland scallop bed at Île du Fantôme, Mingan Islands, in the northern Gulf of St. Lawrence (at 37 m deep in 1990, and 24 m deep in 1991 and 1995). The values for two chlorophyll *a* samples per date are shown for 1995, and the line shows changes in the mean value over time. Black and white circles above the tidal amplitude graph represent new and full moon phases, respectively. Shaded areas delimit spawning periods.

variations involved would likely have been very small since their temperature profiles indicate changes of at most 1°C (from 5 to 6°C) during the most precipitous gonadal drop (between 28 June and 13 July 1968) at 25–30 m in depth. In the second paper, Skreslet (1973) relates spawning to temperature variations of shorter duration than those associated with the tidal cycle. However, he also states that marked temperature variations related to tides occurred prior to spawning and did not induce spawning and that the amplitude of these tidal temperature variations had decreased by the time spawning had begun. Thorarinsdòttir (1993) reports increases in both temperature (8 to 10°C) and in phytoplankton abundance during spawning of *C. islandica* in western Iceland. Thus, the evidence from previous studies that temperature changes account for spawning in *C. islandica* is tenuous, and little attention has been given to alternative hypotheses.

Salinity recorded by the current meter at the 24-m collection site in 1995 showed only slight seasonal fluctuations (30–32‰) and varied little (by 0.32‰) during the abrupt spawning between 8 and 14 August 1995. Salinity changes were likely even less at the 37-m collection site in 1990. Thus, salinity fluctuations on the scallop bed were likely too slight to have acted as cues for the observed abrupt spawnings. Parsons et al. (1992) suggest that the lunar/tidal cycle may act as the spawning cue for *Placopecten magellanicus*. In our study, spawning of *C. islandica* occurred during periods of spring tides, but the amplitude of the tidal changes varied markedly in the 3 years studied. However, spawning did not appear to be related to a particular lunar phase. Our observations also did not suggest that photoperiod controlled spawning, as spawning was 2–3 wk later in 1995 than in 1990 and 1991.

For a number of shallow water invertebrates in temperate and boreal seas, experimental and correlative evidence indicates that the natural spawning cue is the spring phytoplankton bloom (Himmelman, 1981; Starr et al., 1990). Spawning of *Chlamys islandica* in the Mingan Islands is later than the spring bloom as it typically occurs in April-May in this region (Steven, 1974). It is unlikely that the gonads are mature when this event occurs. Histological studies of *C. islandica* in Norway and Iceland show a marked increase in the volume of mature gametes and gonadal size in April, May and June (Sundet & Lee, 1984; Thorarinsdòttir, 1993), and Sundet & Lee (1984) indicate that this development depends on the availability of phytoplanktonic food.

That phytoplankton may trigger spawning in *C. islandica* was first suggested by Thorarinsdòttir (1993) who documented increases in chlorophyll *a* levels (2.0 to 3.5 $\mu g \cdot L^{-1}$) during spawning in 2 consecutive years in Iceland. This hypothesis is further supported by our observations during 3 years in the Mingan Islands (Figure 2). Summer phytoplankton blooms appear to be recurrent events in the northern Gulf of St. Lawrence as they were also documented during 3 consecutive years by Steven (1974). Although phytoplankton was not considered as a potential cue for *C. islandica* spawning in Norway (Skreslet & Brun, 1969; Skreslet, 1973), several studies indicate that a characteristic pattern in northern Norway is a spring diatom bloom in March and April, reduced phytoplankton abundance in May and June, and then a second diatom bloom in July (Gaarder, 1938; Braarud et al., 1958; Heimdal, 1974).

The available data indicate an inconsistent relationship between temperature and spawning in the Iceland scallop. Also, spawning did not appear to be related to day length or to a particular lunar phase, and salinity fluctuations were likely too slight to have acted as cues for the observed abrupt spawnings. Spawning coincided with periods of spring tides in our study and all five spawning events for which phytoplankton abundance was recorded (our study and that of Thorarinsdòttir, 1993) coincided with phytoplankton increases. The latter indicates that spawning may be triggered by summer phytoplankton blooms. Laboratory studies, in which one factor is varied at a time or combinations of factors are varied, are required to evaluate the potential role of phytoplankton, temperature, or other factors in controlling spawning in *C. islandica*.

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THE VELIGER

Argentine Species of *Crassinella* Guppy, 1874 (Bivalvia: Crassatellidae), and Comments on Other Southwestern Atlantic Species

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Abstract. Two species of *Crassinella* Guppy, 1874: *Crassinella maldonadoensis* (Pilsbry, 1897) and *Crassinella marplatensis* Castellanos, 1970 are found in the Argentine malacological province. A third species, *Crassinella lunulata* (Conrad, 1834), extends south to 34°40′S in Uruguay, out of Argentine waters. In the present paper, the shell morphologies of these three species are described. *Crassinella marplatensis* differs from *C. maldonadoensis* in having more central beaks, a definite high trigonal shell outline, and six to eight lamellate surface ribs. The reduction of the anterior right cardinal tooth in *C. maldonadoensis* is also distinctive. Although the morphometric ratios are similar in both species, *C. marplatensis* is consistently higher and flatter than *C. maldonadoensis*. *C. lunulata* is easily distinguished by its high triangular shell outline, beaks at central position, and ventral margin not evenly curved.

INTRODUCTION

According to Harry (1966), nine nominal species of *Crassinella* have been described from the northwestern Atlantic, of which he recognized only two—*Crassinella lunulata* (Conrad, 1834) and *Crassinella martinicensis* (d'Orbigny, 1846)—as valid. Allen (1968) analyzed the functional morphology of *Crassinella mactracea* (Linsley, 1845), a species considered by Coan (1979) as a probable synonym of *C. lunulata*. Vokes & Vokes (1983) reported *C. lunulata* and *C. martinicensis* from the Yucatán Peninsula (Mexico).

The first southwestern Atlantic record of *Crassinella* was from Pilsbry (1897) who described *Crassinella maldonadoensis* (Pilsbry, 1897) from Bahía de Maldonado, Uruguay under *Crassatella* (Lamarck, 1799). Subsequently, Castellanos (1970b) described *Crassinella marplatensis* Castellanos, 1970, based on a single right valve dredged from 38°01′S, 57°26′W (off Mar del Plata, Buenos Aires, Argentina), Scarabino (1977) reported *C. maldonadoensis* from San Matías Gulf, Río Negro, Argentina. Castellanos (1982) extended the known range of *C. marplatensis* to 41°S (off Viedma, Río Negro, Argentina), and erroneously reported the sample of *C. maldonadoensis* here studied, as *C. lunulata*. Rios (1994) reported *C. martinicensis* and *C. lunulata* as distributed north to Santa Catarina and Rio de Janeiro (Brazil), respectively, and *C. marplatensis* as distributed from Rio Grande do Sul (Brazil) to Mar del Plata (Argentina), without any reference to *C. maldonadoensis*.

The present paper reports the results of a recent revision of the malacological collection housed at the Department of Invertebrates, Museo de La Plata (MLP), where an interesting sample of *Crassinella* was found. This allowed the author to redescribe both *C. marplatensis* and *C. maldonadoensis*. *Crassinella lunulata* specimens from southwestern Atlantic waters are also described (Figure 1). Data on shell morphometry, morphometric variability, and periostracum microstructure are also given.

MATERIALS AND METHODS

The present study was undertaken upon the study of collections at the Museo de La Plata (MLP), Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), and Universidade Federal de Juiz de Fora, Brazil (UFJF).

Samples to be studied under scanning electron microscope were carefully cleaned by shaking and brushing the valves in distilled water. Then, they were coated with gold, and appropriately mounted for observation. Shell measurements were made under a stereoscopic microscope provided with a micrometer eyepiece according to the following criteria: shell length (SL): maximum anteroposterior distance; shell height (SH): maximum dorsoventral distance, perpendicular to the anteroposterior axis; shell width (SW): maximum distance across both valves.

RESULTS

Crassinella marplatensis Castellanos

(Figures 2–9)

Crassinella marplatensis Castellanos, 1970b:180, figs. 1–4; 1982:42; Rios, 1994:26, pl. 89, fig. 1276.

Diagnosis: A small *Crassinella* with a triangular, quite compressed, nearly equilateral shell, central beaks moderately opisthogyrate, surface with six to eight lamellate

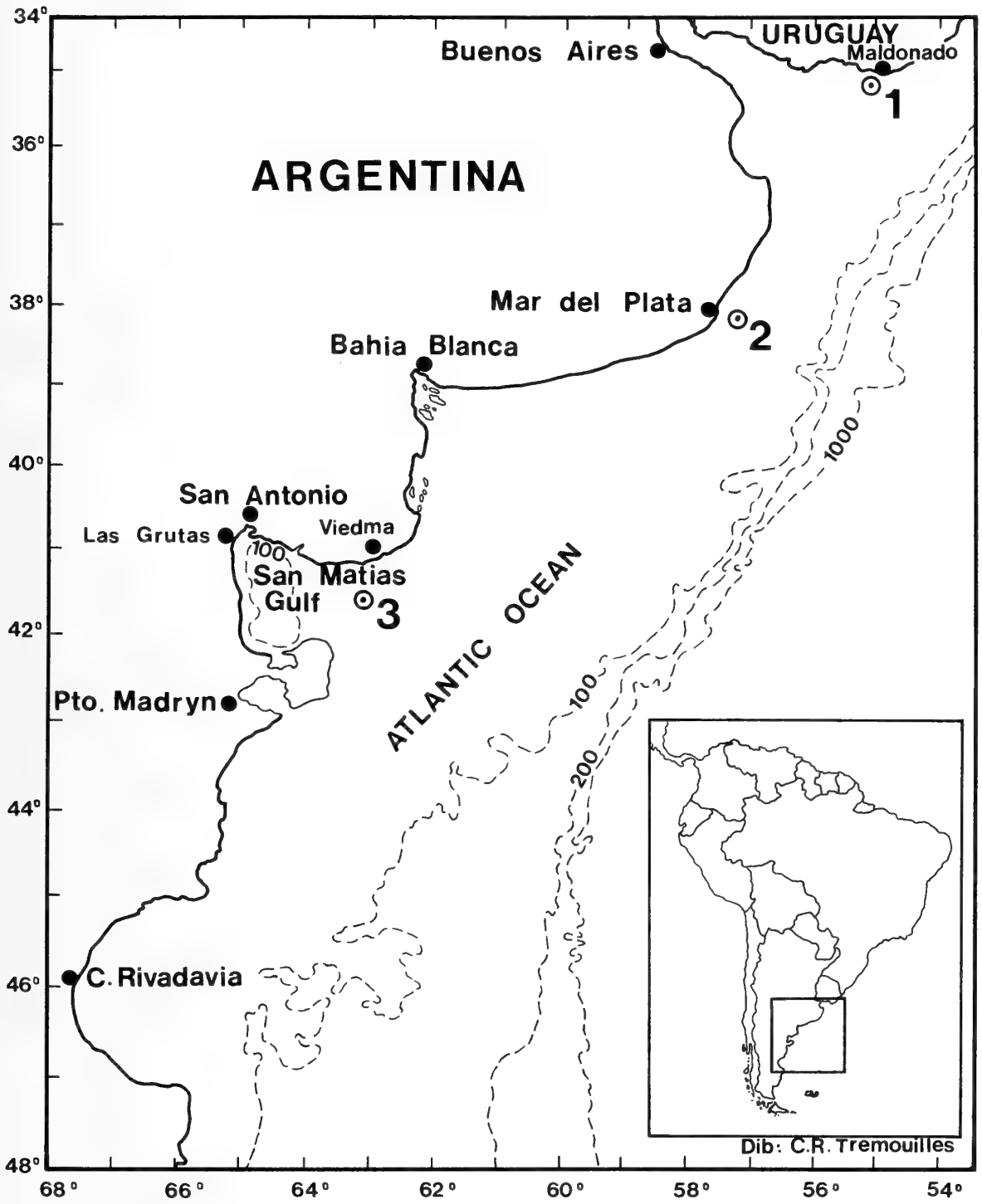
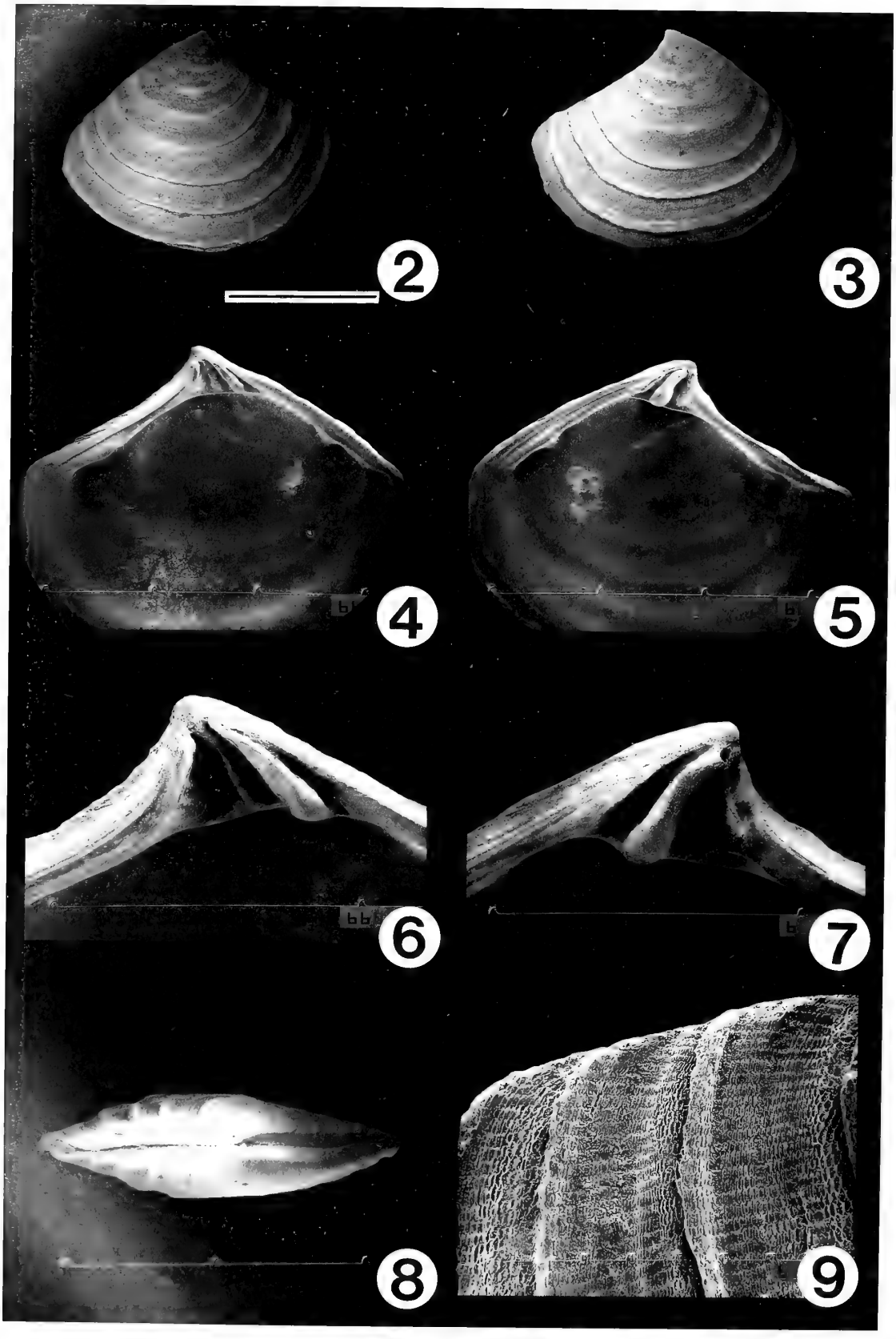


Figure 1

Index map to localities of *Crassinella marplatensis* and *C. maldonadoensis*: 1. Type locality of *C. maldonadoensis*; 2. Type locality of *C. marplatensis*; 3. Source of material reported in the present paper.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commarginal ribs in fully grown specimens, posterodorsal margin straight, anterior end rounded, posterior end acute, ventral margin evenly and sharply arcuate.

Description: Shell small (maximum shell length = 4.3 mm), rather solid, compressed (mean SW/SL = 0.36, [0.30 to 0.40]), outline trigonal (mean SH/SL = 0.83, [0.79 to 0.89]), nearly equilateral, slightly inequivalve. Beaks opisthogyrate, central or slightly displaced backward (located, on average, at 50% of shell length, range: 48–54%). Anterodorsal margin evenly curved. Posterodorsal margin straight, concave near beaks. Ventral margin markedly and uniformly curved. Anterior end rounded, posterior end angulate. Surface sulcated by six to eight commarginal lamellate ribs, separated by wide (approx. 200–250 μm) interspaces. Nepionic shell smooth, well marked, somewhat raised. Escutcheon lanceolate, as long or longer than lunule, well delimited, lacking sculpture, slightly wider in left valve than right one. Lunule elongate, not particularly marked, a little wider in right valve than left one.

Periostracum thick, forming minute elongate hexagonal cells (25 μm wide), arranged in countless radial rows. Periostracal cellules may appear in eroded specimens as opened to exterior.

Hinge plate solid. Left valve: anterior cardinal tooth strong, straight or slightly curved, close to anterodorsal margin. A thin (sometimes enlarged) and low pre-resilial ridge, usually considered as second cardinal tooth. Resilial pit triangular, rather deep. Posterior to resilial pit, lies posterior cardinal tooth, lower and thinner than anterior one. Posterior lateral tooth well developed, cusp triangular, central or little posteriorly displaced. Anterior lateral tooth absent or represented by weak and long ridge separated from dorsal shell margin by very shallow groove. Right valve: anterior cardinal tooth inconspicuous, slender, slightly curved, not reaching base of hinge plate, congruent with anterodorsal margin of shell. Posterior cardinal tooth strong, curved and enlarged at lower end, extending past ventral margin of hinge plate. Posterior to resilial pit, lies a moderately deep socket for left posterior cardinal tooth. Anterior lateral low, cusp triangular, sub-central. Posterior laterals absent, or represented by low ridge forming shallow groove with posterodorsal margin.

Remarks: Previous descriptions of the lateral teeth of *C. marplatensis* are here amended. The posterior right laterals and the anterior left laterals are not double as described by Castellanos (1970b). Also, the left posterior cardinal tooth has been erroneously described (Castellanos, 1970b) as a toothlike projection of the proximal end of the posterior lateral tooth.

Crassinella marplatensis was found (Castellanos, 1970b) to be similar to *C. martinicensis* (d'Orbigny, 1846), from which it differs in being larger and in having fewer commarginal ribs (usually six to eight in contrast with eight to twelve); however, the shape of these ribs is remarkably similar to that described by Harry (1966) for *C. martinicensis*. *C. martinicensis* also differs in having the anterodorsal and posterodorsal margins quite straight, whereas in *C. marplatensis* the anterodorsal margin is slightly convex, and the posterodorsal one shows a sharp concavity immediately behind the beaks, not present in *C. martinicensis*. In this sense, *C. marplatensis* is similar in shell outline and surface sculpture to those juvenile specimens of *C. lunulata* illustrated by Harry (1966:fig. 16). The morphology of the commarginal ribs appears to be close to those of *C. lunulata*, a larger and higher-shelled *Crassinella* species.

C. marplatensis differs from *C. maldonadoensis* in having centrally located beaks, trigonal shell outline, and fewer sharply lamellate commarginal ribs.

Material examined: Twelve specimens (MLP 5110), research vessel *Shinkai Maru*, 9 March 1979, 41°46′S, 63°13′W (off Viedma, Río Negro) in 65 m depth (Figure 1).

Distribution: From Rio Grande do Sul (Brazil) (Rios, 1994) south to 41°S latitude, near Valdés Peninsula (Castellanos, 1982).

Note on the holotype: Castellanos (1970b) reported that the type lot of *C. marplatensis* (a single right valve) was deposited in the malacological collection at the Museo de La Plata. After a careful search, this lot has not been found, and should be considered lost. However, according to the statements in the International Code of Zoological Nomenclature, there is no reason that warrants the selection of a neotype.

Crassinella maldonadoensis (Pilsbry)

(Figures 10–17)

Crassatella (Eriphyla) maldonadoensis Pilsbry, 1897:295; Lamy, 1917:247.

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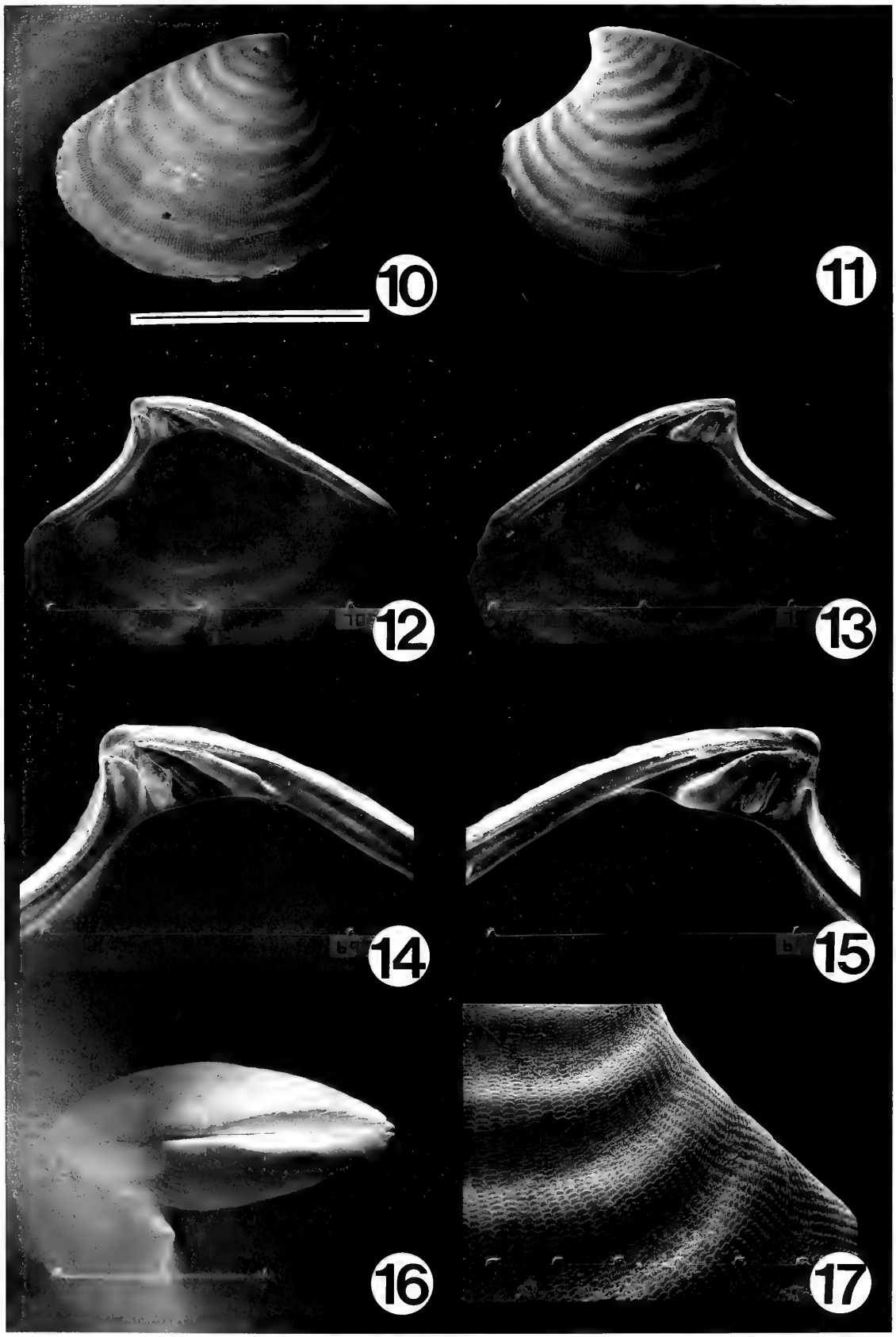
Explanation of Figures 2 to 9

Crassinella marplatensis (MLP 5110) from Viedma, Río Negro, Argentina. 2. Left valve; 3. Right valve; 4. Hinge of the left valve; 5. Hinge of the right valve; 6. Detail of left cardinal teeth; 7. Detail of right cardinal teeth, 8: Dorsal view of the shell; 9. Detail of the periostracal microstructure (scale bars: Figures: 2, 3 (same scale), 8 = 2 mm; Figures 4–7 = 1 mm; Figure 9 = 100 μm).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Crassinella maldonadoensis, Ihering, 1907:450; Castellanos, 1970a:263; 1970b:178, figs. 5–10; Scarabino, 1977:205, pl. 11, fig 2.

Diagnosis: Shell small, compressed, triangular elongate, posterodorsal margin concave, beaks sharply opisthogyrate and displaced posteriorly, posteroventral end protruded, anterior right cardinal tooth reduced, inconspicuous, surface with 10 to 12 rounded commarginal ribs.

Description: Shell small (maximum shell length = 4.8 mm), mean SH/SL ratio = 0.82 (0.75–0.85), compressed (mean SW/SL = 0.37, [0.32–0.47]). Shell outline elongated triangular, posterodorsal margin short, concave (sometimes rather straight at posterior half or straight at its entire length). Anterodorsal margin evenly arcuate. Anterior end acute, posterior end pointed and produced. Ventral margin strongly arcuate. Beaks sharp-pointed, markedly opisthogyrate and posteriorly displaced (located, on average, at 74% of shell length, [67–86%]). Shell with 10 to 12 commarginal ribs, rounded, never lamellated. Periostracum forming multiple radial rows of hexagonal elongate cells (20 μm wide). Shell surface with very pale orange or pink radial strips arranged according to varied patterns.

Hinge plate solid. Hinge: left valve: anterior cardinal tooth strong, high and slender, slightly curved. Anterior resilial ridge (medium cardinal tooth of some authors) thin, very low, straight or slightly curved. Posterior resilial-ridge present, very low. Resilial pit triangular, narrow. Posterior cardinal tooth large and strong. Posterior lateral tooth well defined, triangular, cusp quite low, somewhat distally displaced. Anterior lateral reduced to long and low ridge forming shallow furrow with anterodorsal shell margin itself. Right valve: anterior cardinal tooth weak, hardly distinguishable from anterodorsal margin. Posterior cardinal tooth strong and curved. Posterior end of resilial pit raised. Behind posterior resilial ridge, well-marked socket receives left posterior cardinal tooth. Anterior lateral tooth well developed, cusp low, central or slightly displaced forward. Posterior lateral teeth absent, or represented by long ridge running along inner posterodorsal margin, forming shallow furrow with shell margin. Lunule not well defined, slightly larger in right valve, escutcheon short, cordiform, well marked, sharply concave, slightly larger in left valve.

Remarks: *Crassinella maldonadoensis* differs from *C. marplatensis* in having beaks sharply opisthogyrate and markedly displaced posteriorly; the shell outline is decidedly elongate, and the posterodorsal margin concave (Figure 10). Moreover, in *C. maldonadoensis* the commarginal ribs are smoothly rounded (Figure 17) not lamellated as in *C. marplatensis*. The cardinal teeth are stronger in *C. maldonadoensis*, except for the right anterior cardinal tooth, which is reduced (Figures 14, 15).

Crassinella maldonadoensis was first illustrated by Castellanos (1970b); these specimens show the posterodorsal margin straight or slightly convex, as has been observed in the specimens from La Paloma, Uruguay (MACN part of the lot 31872).

Coan (1984) compared *Crassinella maldonadoensis* with *Crassinella nuculiformis*, an eastern Pacific species, stating that the former has: a more pointed and posteroventrally produced shell outline, a shorter escutcheon, less prominent beaks, and commarginal ribs fading more quickly toward the ventral margin.

Material examined: Twenty specimens (MLP 5111) collected by the research vessel *Shinkai Maru*, 9 March 1979, 41°46′S, 63°13′W (off Viedma, Río Negro) in 65 m depth; numerous specimens (MACN 8634-9) collected by the vessel *Patria* (off Mar del Plata, Buenos Aires) in 8 fathoms depth; numerous specimens (MACN part of the lot 31872), La Paloma (34°40′S, 55°50′W), Rocha, Uruguay (collected from the shore) (Figure 1).

Distribution: *Crassinella maldonadoensis* is known from a few localities: Bahía de Maldonado (type locality), Uruguay (in 5–10 m depth); San Matías Gulf, Argentina: off Viedma, Río Negro (Castellanos, 1970b and present study); Punta San Antonio (Ihering, 1907); and off Las Grutas, 40°54′S, 65°01′W, Río Negro (Scarabino, 1977). The MACN lot from La Paloma (34°40′S, 55°50′W), reported above, is the northernmost known locality for *C. maldonadoensis*.

Crassinella lunulata (Conrad)

(Figures 18–25)

Astarte lunulata Conrad, 1834:133, not figured
Thetis parva C.B. Adams, 1845:9, not figured
Astarte mactracea Linsley, 1845:275, text fig.
Crassatella guadalupensis d'Orbigny, 1846:289, pl. 27, figs. 24–26
Astarte pfeifferi Philippi, 1848:133, not figured
Gouldia fastigiata Gould, 1862:282, not figured
Eriphyla galvestonensis Harris, 1895:8, pl. 1, figs. 2a,b

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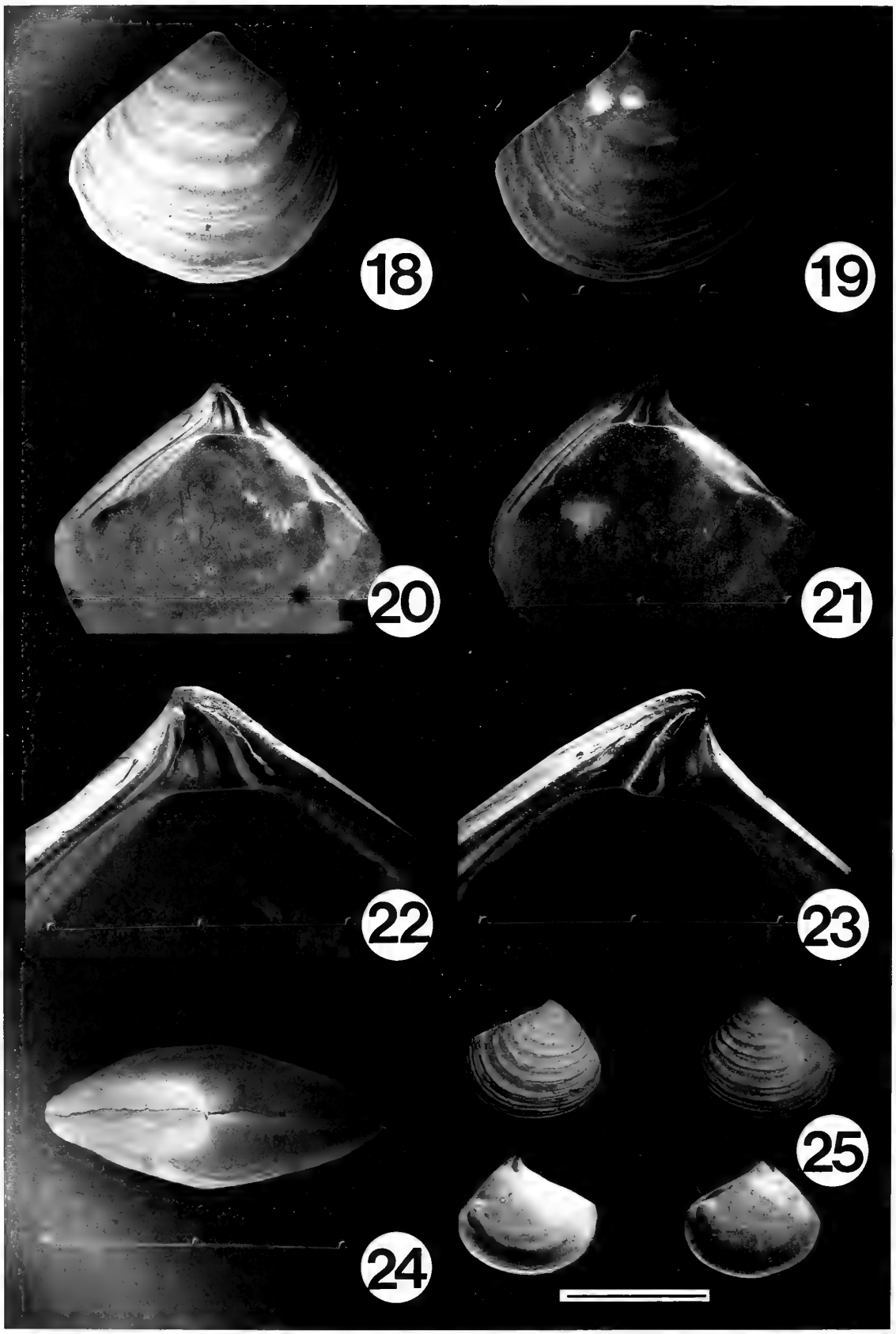
Explanation of Figures 10 to 17

Crassinella maldonadoensis (MLP 5111) from Viedma, Río Negro, Argentina. 10. Left valve; 11. Right valve; 12. Hinge of the left valve; 13. Hinge of the right valve; 14. Detail of left cardinal teeth; 15. Detail of right cardinal teeth; 16. Dorsal view of the shell; 17. Detail of the periostracal microstructure (scale bars: Figures 10, 11 (same scale) = 2 mm; Figures. 12–16 = 1 mm; Figure 17 = 100 μm).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Crassinella oregonensis Keen, 1938:31, p1.2, figs. 11–12
Crassinella lunulata, Harry, 1966:11, figs. 6, 7, 13, 15–17
Crassinella mactracea, Allen, 1968:38, figs. 1–5

Diagnosis: Shell high triangular, nearly equilateral and slightly inequivalve, moderately inflated (length about 2.3 × width). Posterodorsal margin straight, anterodorsal margin straight or faintly curved. Ventral margin strongly convex, its posterior half being consistently more sharply curved than the anterior one. Shell somewhat protruded postero-ventrally.

Description: Shell small (maximum shell-length = 5.25 mm), triangular, slightly inequilateral, high (mean SH/SL = 0.89, [0.85–0.95]), not much compressed (mean SW/SL = 0.43, [0.42–0.46]). Beaks opisthogyrate, centrally located or slightly displaced to either direction. Anterior margin evenly and slightly convex. Posterodorsal margin straight in the right valve (Figures 19, 25) and somewhat humpbacked in the left one (Figures 18, 25), forming right angle with anterodorsal margin. Ventral margin strongly arcuate. Curvature of posterior half of ventral margin more acute than anterior half, endowing distinctive shape to shell outline. Shell sculptured with 12 to 14 commarginal raised ribs in adults, somewhat variable in shape but neither strictly lamellated nor rounded. (Figure 25). Hinge: right valve: anterior cardinal low, not projecting from anterior margin, posterior cardinal strong, central, not extending past ventral margin of hinge plate. Resilial pit deep, very slightly raised at posterior end. Narrow socket to receive left posterior cardinal tooth. Anterior lateral tooth well developed, triangular, high. Along inner posterior lateral margin, slight depression to receive left posterior lateral. Left valve: anterior cardinal wedge-shaped, faintly curved. Posterior cardinal well developed. Resilial pit deep, anterior margin raised in strong ridge, posterior margin barely marked by weak ridge. Posterior lateral tooth well developed, triangular, cusp central, or slightly displaced forward, pointed. Escutcheon sharply delimitated, wider in right valve. Lunule narrow, slightly wider in left valve (Figure 24). When viewed laterally, postero-dorsal margin of left valve is characteristically higher than right one.

Remarks: *C. lunulata* can be differentiated from *C. marplatensis* and *C. maldonadoensis* in having a definite high triangular shell shape, shell equilateral or slightly shorter at the anterior end, with the ventral margin strongly arcuate, with its posterior half more acutely curved. The lateral teeth are comparatively better developed. The number of commarginal ribs is greater in *C. lunulata*.

Material examined: Three specimens (UFJF 5906) Cabo Frio, Rio de Janeiro (23°S approx.), Brazil; one specimen (UFJF 5178) Cabo Frio, Rio de Janeiro, Brazil; 12 loose valves (UFJF 5568) Jaraguá, Maceió (09°30′S approx.), Alagoas, Brazil (in all cases specimens were collected from the shore); one specimen (MACN part of the lot 31872) La Paloma (34°40′S, 55°50′W), Department of Rocha, Uruguay).

Distribution: *C. lunulata* ranges from Bermuda (Rios, 1994) to La Paloma (34°40′S), Uruguay (present study).

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The kind cooperation of Prof. Hugo Irigoyen (MACN) and Dr. Maury Pinto de Oliveira (UFJF) for supplying specimens, and Dr. Eugene Coan for providing bibliography, is here acknowledged. The author is greatly indebted to Guido Pastorino for his continuing support.

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Explanation of Figures 18 to 25

Crassinella lunulata. Figures 18–24: specimens from La Paloma, Rocha, Uruguay (MACN part of the lot 31872); 18. Left valve; 19. Right valve; 20. Hinge of the left valve, 21. Hinge of the right valve, 22. Detail of left cardinal teeth; 23. Detail of right cardinal teeth; 24. Dorsal view of the shell; Figure 25. Inner and outer view of a specimen from Cabo Frio, Rio de Janeiro, Brazil (UFJF 5906). (scale bars: Figures 18–21, 24 = 2 mm; Figures 22–23 = 1 mm; Figure 25 = 5 mm).

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THE VELIGER

Deep-Sea Vesicomyid Clams from Hydrothermal Vent and Cold Seep Environments: Analysis of Shell Microstructure

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Abstract. The shell structure of five vesicomyid clams (i.e., *Vesicomya* species A, *V.* species B, *V.* species C, *V.* species D, and *V.* species E) from deep-sea hydrothermal vent and cold sulfide/methane seep environments is characterized by scanning electron microscopy (SEM). SEM examination of fractured and sectioned specimens reveals an array of shell microstructures in distinct arrangements. The shell of *V.* species A contains the most layers (7) and exhibits microstructure patterns markedly different than those of the other four vesicomyid species. The shell microstructure patterns of *V.* species B and *V.* species C, although similar, also show important differences. For example, fine spherulitic structure is exclusively found in *V.* species B, and "coarse" complex crossed lamellar structure only occurs in *V.* species C. *Vesicomya* species D and *V.* species E likewise exhibit similar shell microstructure patterns, although *V.* species D has an inner fine complex crossed lamellar layer not found in *V.* species E, and *V.* species E has an inner irregular complex crossed lamellar layer not present in *V.* species D. The shell microstructure patterns in the aforementioned species vary from those of previously described deep-sea vesicomyids (i.e., *Calyptogena magnifica* Boss & Turner, 1980; *C. phaseoliformis* Métivier, Okutani & Ohta, 1986; and *C.* cf. *pacifica* Dall, 1891). Results of these investigations indicate that shell microstructure analysis may be of great value in taxonomic studies of the Vesicomyidae.

INTRODUCTION

The systematic relationships of vesicomyid clams from deep-sea hydrothermal vent and cold sulfide/methane seep environments are beset with problems, primarily because of the dearth of samples thoroughly analyzed and their considerable morphologic variability. Although the vicissitudes and high costs of sampling in these extreme environments impeded early systematic work on the group, more recent collections have yielded relatively large numbers of specimens from a wide range of sulfide-rich, deep-sea sites (Tunnicliffe, 1991; Kennish & Lutz, 1992; Lutz & Kennish, 1993; Lutz et al., 1994). In 1996, the shell microstructures of three vesicomyid species from deep-sea hydrothermal vent and cold sulfide/methane seep environments (*Calyptogena magnifica* Boss & Turner, 1980; *C. phaseoliformis* Métivier, Okutani & Ohta, 1986; and *C.* cf. *pacifica* Dall, 1891) were described with the primary purpose of providing important new information for taxonomic differentiation of members of the group (Kennish et al., 1996). Here, the shell microstructure of five additional vesicomyid species from these unusual environments is characterized by scanning electron microscopy (SEM). We are providing a new suite of data from these microstructure studies to bring to bear for systematic analysis.

MATERIALS AND METHODS

Ten vesicomyid clams ranging in length from 5.0–18.5 cm (Table 1) were collected alive in 1994 via submersible net sampling from hydrothermal vent fields at Middle Valley on the Juan de Fuca Ridge (4 specimens; *Alvin* Dives 2803 and 2805 at 48°27.40′N and 48°27.25′N, respectively) and the Guaymas Basin in the Gulf of California (3 specimens; *Alvin* Dive 2839 at 27°34.85′N), as well as from cold sulfide seeps in the Oregon Subduction Zone (3 specimens; *Alvin* Dive 2796 at 44°40.53′N) (Table 1). The soft tissues of the clams were excised and frozen at −70°C. However, they were not examined histologically, and the sex and stage of development of the clams were not determined. The shells of the specimens were air dried, carefully packaged, and returned to the laboratory for detailed analysis. Voucher specimens were deposited in the Rutgers University Geology Museum in New Brunswick, New Jersey.

Five of the specimens were prepared for SEM examination by fracturing and sectioning their shells in the laboratory. Subsequent to fracturing, shell fragments were sonicated in distilled water, dehydrated in 95% ethanol, air dried, and coated with gold/palladium prior to observation in an Amray 18301 SEM (preparation 1). Sectioned shells were prepared by polishing and etching

Table 1

Size measurements of vesicomyid clams collected at sampling sites in the eastern Pacific Ocean and Gulf of California.

Location	Specimen no.	Species	Length (cm)
Middle Valley[a]	1	*Vesicomya* species A	14.0
	2	*Vesicomya* species A	14.4
	3	*Vesicomya* species A	18.5
	4	*Vesicomya* species D	12.8
Guaymas Basin[b]	5	*Vesicomya* species B	8.0
	6	*Vesicomya* species D	9.6
	7	*Vesicomya* species E	10.1
Oregon Subduction Zone	8	*Vesicomya* species C	6.2
	9	*Vesicomya* species D	5.0
	10	*Vesicomya* species D	7.0

[a] Juan de Fuca Ridge.
[b] Gulf of California.

them with 6% HCL. After being etched, the polished sections were rinsed with distilled water, dehydrated in 95% ethanol, air dried, and coated with gold/palladium prior to observation in the SEM (preparation 2).

RESULTS

Vesicomya Species A

Specimens of *Vesicomya* species A were collected from Middle Valley, Juan de Fuca Ridge, on 24 July and 26 July 1994. The shell of this species is composed of seven layers. Proceeding from the shell exterior inward, these layers consist of the following structural types: (1) outer homogeneous, (2) planar spherulitic, (3) "fine" irregular spherulitic, (4) fine complex crossed lamellar, (5) irregular simple prismatic (adductor and pallial myostracum), (6) inner "fine" vertical non-denticular composite prismatic, and (7) inner homogeneous (Figures 1–6).

Vesicomya Species B

This species was recovered during benthic sampling in the Guaymas Basin on 8 October 1994. The thin shell of *Vesicomya* species B consists of several characteristic layers: (1) outer homogeneous structure, (2) fine spherulitic structure, (3) fine complex crossed lamellar structure, (4) irregular simple prismatic structure (adductor and pallial myostracum), and (5) inner fine complex crossed lamellar structure (Figures 7–9). The adductor and pallial myostracum can be traced down to the fine complex crossed lamellae composing the inner shell layer. As such, this skeletal sequence differs markedly from that in *V.* species A, which is composed of "fine" vertical non-denticular composite prismatic and inner homogeneous layers below the myostracum.

Vesicomya Species C

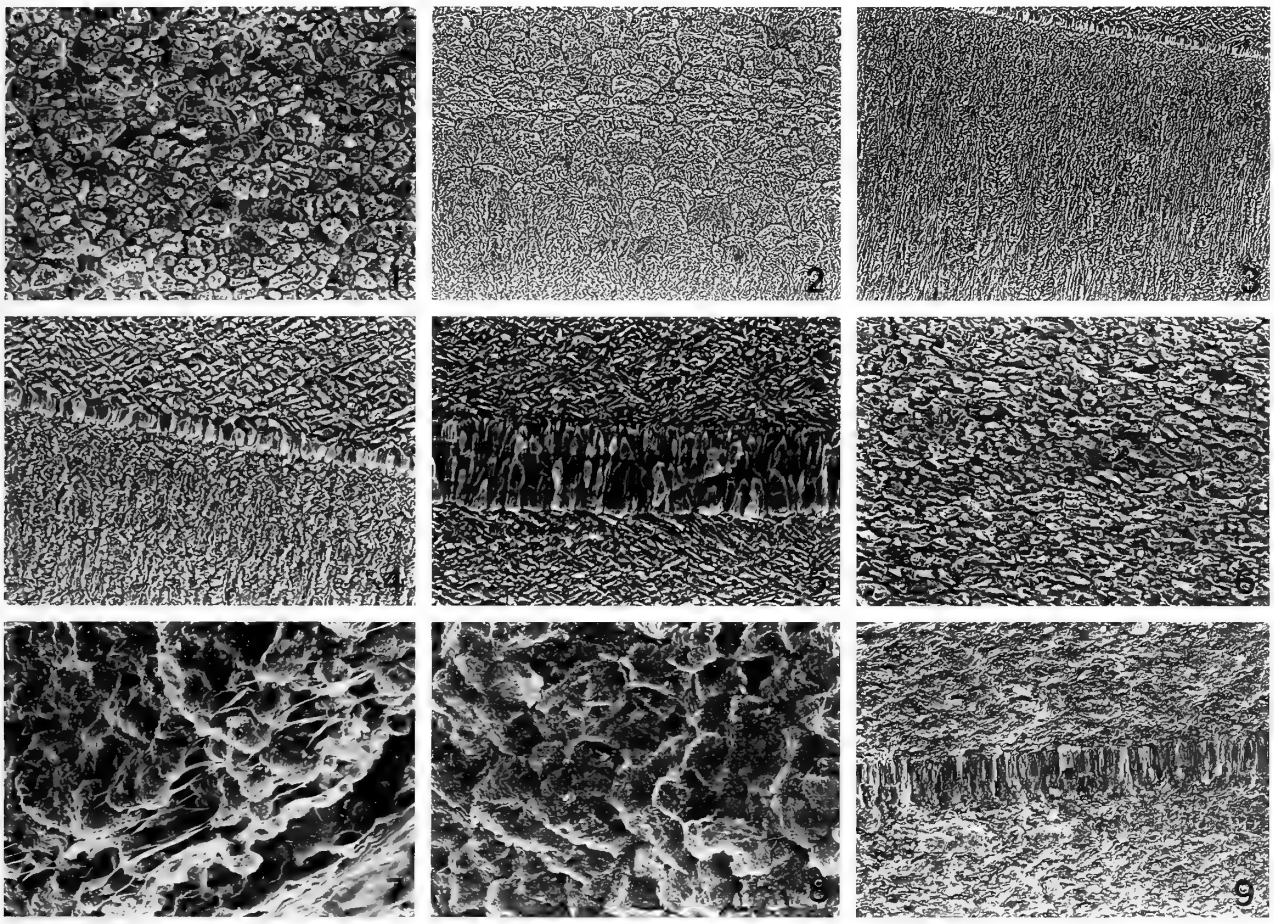
Collected in the Oregon Subduction Zone on 16 July 1994, *Vesicomya* species C has a skeletal sequence similar to that of *V.* species B. The shell of this species is composed of six layers: (1) outer homogeneous structure, (2) fine complex crossed lamellar structure, (3) irregular simple prismatic structure (adductor and pallial myostracum), (4) "coarse" complex crossed lamellar structure, (5) "fine" vertical non-denticular composite prismatic structure, and (6) inner fine complex crossed lamellar structure (Figures 10–12). The "coarse" complex crossed lamellar layer is found exclusively in this species (Figure 11). It appears similar to fine complex crossed lamellar structure, as defined by Carter (1990), albeit with larger structural subunits.

Vesicomya Species D

Vesicomya species D was collected in the Guaymas Basin on 8 October 1994. Vertical sections of polished and acid-etched specimens of this species exhibit four shell layers: (1) outer homogeneous structure, (2) fine complex crossed lamellar structure, (3) "fine" irregular simple prismatic structure (adductor and pallial myostracum), and (4) inner fine complex crossed lamellar structure (Figures 13–15). Typically, there are alternating adductor myostracal layers in this species. *Vesicomya* species D does not contain the fine spherulitic structural layer observed in *V.* species B, or the "coarse" complex crossed lamellar and "fine" vertical non-denticular composite prismatic layers found in *V.* species C.

Vesicomya Species E

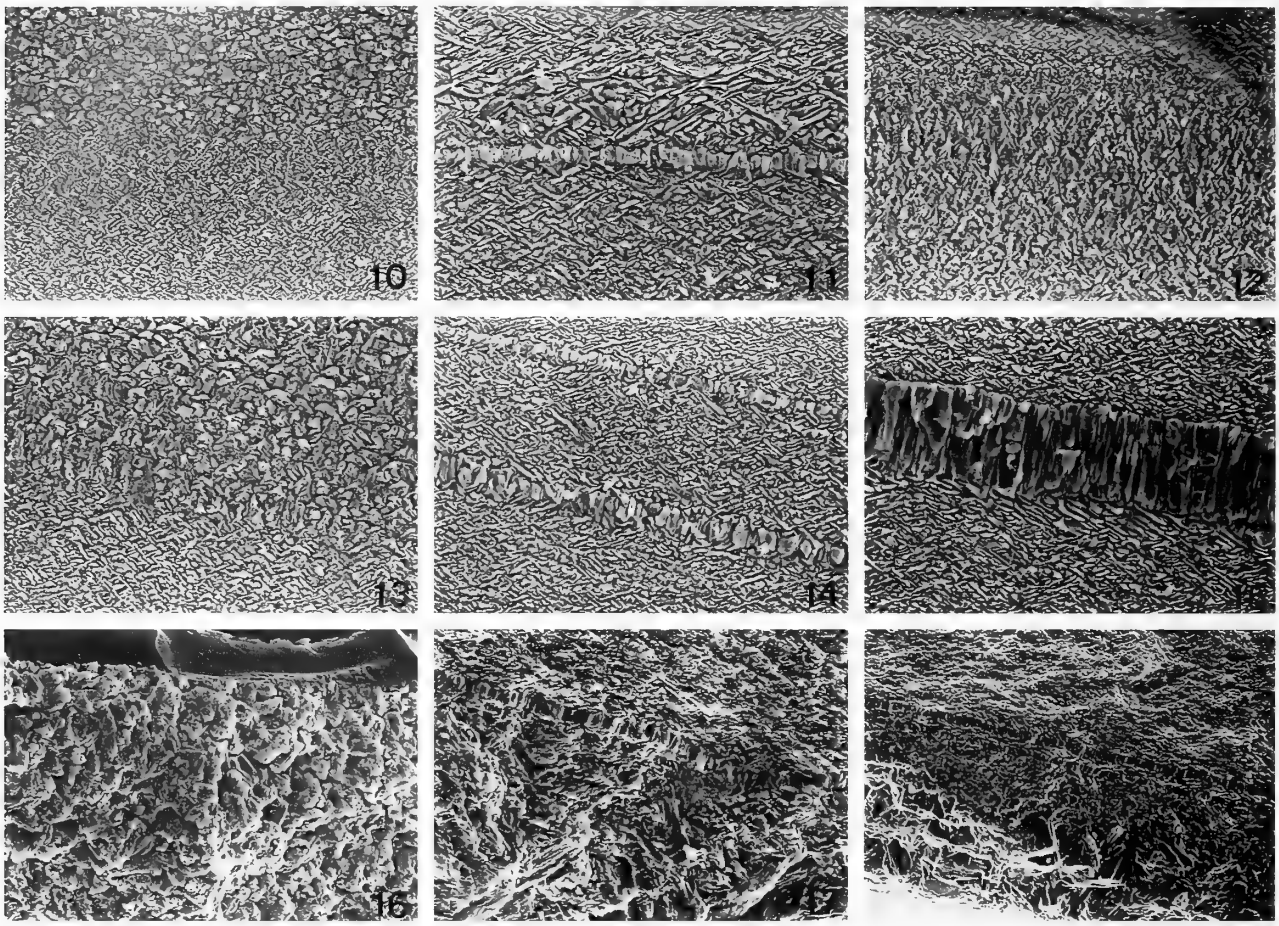
Also collected in the Guaymas Basin on 8 October 1994, *Vesicomya* species E is characterized by five shell



Explanation of Figures 1 to 9

Figure 1. *Vesicomya* species A. Radial section, preparation 2. Umbo toward the left. External shell surface toward the top. Homogeneous structure. Horizontal field width (HFW) = 52 μm. Figure 2. *Vesicomya* species A. Radial section, preparation 2. Umbo toward the left. External shell surface toward the top. Planar spherulitic structure overlies "fine" irregular spherulitic structure. The border of the latter blends with fine complex crossed lamellar structure. HFW = 104 μm. Figure 3. *Vesicomya* species A. Radial section, preparation 2. Umbo toward the right. External shell surface toward the top. Outer fine complex crossed lamellar structure separated from inner "fine" vertical non-denticular composite prismatic structure by irregular simple prismatic structure (pallial myostracum). HFW = 104 μm. Figure 4. *Vesicomya* species A. Radial section, preparation 2. Umbo toward the right. External shell surface toward the top. Magnified portion of Figure 3 showing outer fine complex crossed lamellar structure separated from inner "fine" vertical non-denticular composite prismatic structure by irregular simple prismatic (pallial myostracum) structure. HFW = 52 μm. Figure 5. *Vesicomya* species A. Radial section, preparation 2. Umbo toward the left. External shell surface toward the top. Irregular simple prismatic structure (adductor myostracum) is embedded in fine complex crossed lamellar structure. HFW = 52 μm. Figure 6. *Vesicomya* species A. Radial section, preparation 2. Umbo toward the right. External shell surface toward the top. Inner homogeneous structure. HFW = 52 μm. Figure 7. *Vesicomya* species B. Vertical fracture, preparation 1. Umbo away from the reader. External shell surface toward the top. Homogeneous structure. HFW = 52 μm. Figure 8. *Vesicomya* species B. Vertical fracture, preparation 1. Umbo away from the reader. External shell surface toward the top. Fine spherulitic structure. HFW = 52 μm. Figure 9. *Vesicomya* species B. Vertical fracture, preparation 1. Umbo away from the reader. External shell surface toward the top. Irregular simple prismatic structure (adductor and pallial myostracum indistinguishable) is embedded in fine complex crossed lamellar structure. HFW = 52 μm.

layers. Proceeding from the outer shell surface inward, these layers consist of: (1) outer homogeneous structure, (2) fine complex crossed lamellar structure, (3) irregular simple prismatic structure (adductor and pallial myostracum), (4) fine complex crossed lamellar structure, and (5) inner irregular complex crossed lamellar structure (Figures 16–18). This structural arrangement is similar to that of *V.* species D.



Explanation of Figures 10 to 18

Figure 10. *Vesicomya* species C. Vertical section, preparation 2. Umbo toward the reader. External shell surface toward the top. Outer homogeneous structure (above) blends with fine complex crossed lamellar (below). HFW = 52 μm. Figure 11. *Vesicomya* species C. Vertical section, preparation 2. Umbo toward the reader. External shell surface toward the top. Irregular simple prismatic structure (pallial myostracum) separates fine complex crossed lamellar structure above from "coarse" complex crossed lamellar structure below. HFW = 52 μm. Figure 12. *Vesicomya* species C. Vertical section, preparation 2. Umbo toward the reader. External shell surface toward the top. "Fine" vertical non-denticular composite prismatic structure is embedded in fine complex crossed lamellar structure. HFW = 52 μm. Figure 13. *Vesicomya* species D. Radial section, preparation 2. Umbo toward the right. External shell surface toward the top. Thin "fine" irregular simple prismatic (pallial myostracum) structure separates outer homogeneous structure (above) and inner fine complex crossed lamellar structure (below). HFW = 52 μm. Figure 14. *Vesicomya* species D. Radial section, preparation 2. Umbo toward the right. External shell surface toward the top. Two irregular simple prismatic structures embedded in fine complex crossed lamellar structure. This is the result of the splitting of adductor myostracum. HFW = 52 μm. Figure 15. *Vesicomya* species D. Radial section, preparation 2. Umbo toward the right. External shell surface toward the top. Irregular simple prismatic structure (adductor myostracum) embedded in fine complex crossed lamellar structure. HFW = 52 μm. Figure 16. *Vesicomya* species E. Vertical fracture, preparation 1. Umbo toward the reader. External shell surface toward the top. Homogeneous structure beneath the periostracum. HFW = 52 μm. Figure 17. *Vesicomya* species E. Vertical fracture, preparation 1. Umbo toward the reader. External shell surface toward the top. Irregular simple prismatic structure (pallial myostracum) separates outer fine complex crossed lamellar structure from inner irregular complex crossed lamellar structure. HFW = 52 μm. Figure 18. *Vesicomya* species E. Radial fracture, preparation 1. Umbo toward the right. External shell surface toward the top. Two layers of irregular simple prismatic structure are embedded in fine complex crossed lamellar structure. Irregular complex crossed lamellar structure composes the innermost shell layer. HFW = 104 μm.

Table 2

Summary of shell microstructure layers in vesicomyid clams from deep-sea hydrothermal vent and cold sulfide/methane seep environments.

Shell layer	Species							
	A[a]	B[b]	C[c]	D[d]	E[e]	CM[f]	CP[g]	CcfP[h]
Outer homogeneous	√	√	√	√	√		√	
Irregular simple prismatic	√	√	√	√	√	√	√	√
"Fine" vertical non-denticular composite prismatic	√		√					√
Fine complex crossed lamellar	√	√	√	√	√	√	√	√
"Coarse" complex crossed lamellar			√					
"Fine" irregular spherulitic	√							
Irregular spherulitic prismatic							√	
Fine spherulitic		√						
Planar spherulitic	√					√	√	√
Inner homogeneous	√							
Inner fine complex crossed lamellar		√	√	√				
Inner irregular complex crossed lamellar					√			
Inner cone complex crossed lamellar					√			

[a] *Vesicomya* species A.
[b] *Vesicomya* species B.
[c] *Vesicomya* species C.
[d] *Vesicomya* species D.
[e] *Vesicomya* species E.
[f] *Calpytogena magnifica.*
[g] *Calyptogena phaseoliformis.*
[h] *Calyptogena* cf. *pacifica.*
√ = present.

DISCUSSION

The systematic relationships of the family Vesicomyidae (*Calyptogena* and *Vesicomya*) remain uncertain. The considerable variability of taxa, insufficient anatomical data available, and the ill-defined boundaries of heterodont bivalves with which the vesicomyids have been associated (Boss & Turner, 1980; Kennish & Lutz, 1992; Kennish et al., 1996), hinder systematic work on the group. The past effort by various taxonomists to place many genera and species, now included in the Vesicomyidae, in other families (i.e., Arcticidae [Cryprinidae], Carditidae, Kelliellidae, and Veneridae) is testimony to the difficulties encountered in classifying the vesicomyids. However, as collections of specimens from hydrothermal vents and cold-sulfide/methane seeps mount, a clearer picture of the systematic relationships of the Vesicomyidae should emerge. Living or dead specimens of vesicomyids have now been collected or photographed from hydrothermal vents or cold-sulfide seeps in the eastern Pacific (Explorer Ridge, Juan de Fuca Ridge, Gorda Ridge, Santa Barbara Channel, Monterey [Ascension Canyon], Guaymas Basin, Galapagos Rift and 21°N, 13°N, 11°N, 9–10°N, and 17–22°S along the East Pacific Rise), Sea of Japan, Aleutian Trench, Gulf of Mexico (Florida Escarpment, Louisiana Slope, and Alaminos Canyon), and Laurentian Fan (Swinbanks, 1985; Turner, 1985a, b; Lutz & Kennish, 1993; Kennish et al., 1996).

Comparative studies of the shell microstructure of vesicomyids from hydrothermal vents and cold-water sulfide seeps are ongoing. Data are being collected on both fractured and sectioned specimens in various orientations utilizing SEM. These studies are providing a higher-resolution record of the basic constructional units of the shells.

Vesicomya species A–E share a number of common shell microstructural features, and they exhibit several important differences (Table 2). *Vesicomya* species A contains more shell layers (7) than the other four vesicomyid species (Figures 1–6). *Vesicomya* species A and *V.* species B are the only two vesicomyid forms examined in this study that have spherulitic shell structure. Planar spherulitic structure in *V.* species A compares favorably

with that described by Kennish et al. (1996) in *Calyptogena magnifica*. It consists of horizontally flattened spherulites that are quite variable in shape and measure about 1–7 μm in width. The spherulites have highly irregular contacts, yielding a layer with no particular structural arrangement. Planar spherulitic structure appears similar to fine to coarse homogeneous structure with which it may be confused. Aside from the spherulitic microstructures, "fine" vertical non-denticular composite prismatic structure occurs in *V.* species A (Figure 4) and has also been found in *V.* species C (Figure 12). The innermost homogeneous layer observed in *V.* species A (Figure 6) is not present in the other vesicomyids.

Vesicomya species B has five shell layers, and *V.* species C, six shell layers (Table 2) (Figures 7–12). A fine spherulitic layer occurs in *V.* species B between the outer homogeneous and fine complex crossed lamellar layers (Figures 7–9), but it is not found in *V.* species C. In contrast, "coarse" complex crossed lamellar and "fine" vertical non-denticular composite prismatic layers occur in *V.* species C (Figures 11–12), but not in *V.* species B. *Vesicomya* species D has only four shell layers (Figures 13–15), being devoid of fine spherulitic structure observed in *V.* species B and "fine" vertical non-denticular composite prismatic and "coarse" complex crossed lamellar structures encountered in and *V.* species C (Table 2).

Vesicomya species E contains five shell layers in a sequence similar to that of *V.* species D (Figures 16–18). However, the inner irregular complex crossed lamellar layer in *V.* species E (Figure 17) does not occur in *V.* species D, and the inner fine complex crossed lamellar layer in *V.* species D (Figure 13) is not found in V. species E. Variation in the relative thicknesses of the shell layers in these two species—as well as in all the vesicomyids investigated in this study—can be substantial, thereby accounting for much of the difference observed in the overall shell thicknesses of members of the family.

It is important to note that the arrangement of shell layers can also vary considerably from one part of a vesicomyid shell to another, owing to alternating adductor myostraca, dissolution, or other effects. While a complete sequence of layers may be observed in some areas of the shell, one or more layers can be locally missing. Hence, it is necessary to carefully examine the entire shell when assessing the microstructure patterns of this complex group.

The shell structure of the five vesicomyid species examined in this study differs from that of the three previously described vesicomyids (i.e., *Calyptogena magnifica*, *C. phaseoliformis*, and *C.* cf. *pacifica*) (Kennish et al., 1996) (Table 2). The shell of *C. magnifica* consists of layers of planar spherulitic, fine complex crossed lamellar, inner cone complex crossed lamellar, and irregular simple prismatic structure, and that of *C. phaseoliformis* is composed of layers of fine homogeneous, planar spherulitic, fine complex crossed lamellar, irregular spherulitic prismatic, and irregular simple prismatic structure. In *C.* cf. *pacifica*, the shell contains layers of planar spherulitic, fine complex crossed lamellar, vertical non-denticular composite prismatic, and irregular simple prismatic structure (Kennish et al., 1996). Results of this study suggest that the shell microstructure of members of the Vesicomyidae can vary considerably and therefore may be of great value in systematic studies of the group.

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THE VELIGER

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Inducible Phenotypic Plasticity of the Radula in *Lacuna* (Gastropoda: Littorinidae)

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Abstract. The radula is the major feeding organ of most gastropods and is a key taxonomic feature for many species. I demonstrate that two species of snail in the genus *Lacuna* Turton, 1827 (Gastropoda: Littorinidae) produce differently shaped radular teeth when fed different foods, displaying intraspecific variability as extreme as would usually be considered to define different species. The new tooth morphology is produced on the non-feeding end of the constantly regenerating radula, and is thus different from use-induced feeding morphologies seen in arthropods or vertebrates. Tooth shape in *Lacuna* is phenotypically plastic, inducible with different food conditions, and reversible within an individual's lifetime, allowing rapid response to new environmental conditions.

INTRODUCTION

Gastropod species identity and taxonomy traditionally has been based on a wide variety of soft body and shell characteristics. The shell is used for taxonomic purposes both in extant and extinct species as it preserves well and is abundant in fossil deposits. However, many aspects of the shell shape and decoration are variable within species, and several have been shown to be phenotypically plastic (Appleton & Palmer, 1988). The gastropod radula is widely regarded as being a reliable character for species identity, and is commonly considered to be species specific. For example, Fretter & Graham (1994: 162) state, regarding the radula, that "the ribbon bears teeth placed regularly along side one another . . . . and the number of these and the shape of the teeth differ from species to species, though remaining fairly constant within one species. As a consequence of this and the fact that they are imperishable and may be extracted from dried bodies, the radula is an important organ from the taxonomic view." Because the radula is a major feeding organ of most gastropods, we might predict close associations between diet and radular form (Padilla, 1985, 1989). In fact, ontogenetic changes in diets of some species of *Conus* have been shown to be correlated with ontogenetic changes in radular morphology (Nybakken, 1990).

In the northeastern Pacific, snails in the genus *Lacuna* Turton, 1827, are important grazers of macroalgae, including kelp, and are the dominant grazers in many eelgrass communities (Martel, 1990; Martel & Chia, 1991a, b). These snails readily move between these two habitats as planktonic larvae (> 4 weeks as planktotrophic larvae) or as juveniles and adults which use mucus threads to parachute in water currents (Martel & Chia, 1991b, c). The shapes of radular teeth most effective at grazing on these two different types of foods will be very different (Padilla, 1985, 1989). *Lacuna* feeding on kelps and other macrophytes excavate the algal tissue itself. Pointed teeth are more effective at gouging this type of surface due to mechanical factors such as stress concentration at tooth tips as compared to broad tooth cusps (Padilla, 1985). In eelgrass beds, however, *Lacuna* graze on the epiphytic micro and filamentous algae growing on the surface of the grass blades without damaging the tissues of the grass beneath. Blunt teeth would be more effective at scraping epiphytes from a surface. Feeding efficiency on these two very different substrata may therefore be a strong selective force on radular tooth morphology (Hickman, 1980; Padilla 1985, 1989).

In initial observations, I found individuals of *Lacuna vincta* (Montagu, 1803) and *L. variegata* Carpenter, 1864, collected from kelp had pointed radular teeth, whereas those collected in eelgrass possessed blunt teeth. These differences could be due to several factors: (1) animals could change their diet ontogenetically and have an ontogenetic shift in radular tooth shape as is seen in *Conus*; (2) *Lacuna vincta* and *L. variegata* populations could be polymorphic for tooth shape—different individuals could have different radular morphologies, and move to habitats that match their tooth shape; or (3) tooth shape could be phenotypically plastic, and inducible by cues from the animal's food or environment (Bradshaw, 1965; Smith-Gill, 1983). I conducted experiments to test whether tooth morphology in an adult snail could change in response to the diet of these snails.

MATERIALS AND METHODS

Lacuna variegata and *L. vincta* (males and females, 2.5–9 mm shell length) were collected from several different kelp beds and eelgrass beds near the Friday Harbor Laboratories, San Juan Island, Washington. Flow-through

Table 1

Radular tooth shape of snails reared on kelp or epiphyte covered eelgrass for 8 weeks. The results of a 3-way G test showed that for *Lacuna vincta* and *L. variegata* food had a significant effect on tooth form ($P < 0.001$), and the two species did not differ in their response.

Food	Epiphytes	Kelp
Lacuna vincta		
Pointed Teeth	0%	100%
Blunt Teeth	100%	0%
Lacuna variegata		
Pointed Teeth	0%	100%
Blunt Teeth	100%	0%

seawater tanks were filled with either epiphyte-covered eelgrass (*Zostera marina*) or kelp (*Laminaria groenlandica*). The snails from each species were randomly assigned to one of two environment/food conditions, kelp or epiphyte-covered eelgrass. Snails were housed in plastic cages with 1 mm plastic screening replacing four sides (eight different cages for each food/habitat type), and fed fresh food every 3 to 4 days, before all of the kelp or epiphytes provided were consumed. After 8 weeks, I sacrificed one animal of each species from each cage, dissected their radulae, and cleaned them in a mild chlorine solution with very gentle sonication without heat (Norelco Razormate). The cleaned radulae were dehydrated with 2,2, Dimethoxy-propane and mounted flat with dual adhesive tape on aluminum stubs.

Both species replace their radula at a rate of around three rows per day, and completely replace their radula in around 3 to 4 weeks (Padilla et al., 1996). Therefore, all individuals would have completely replaced the teeth on the radula at least once during the experiment. Radulae of eight individuals for each species in each treatment were examined with a scanning electron microscope to determine the shapes of the teeth. The shapes of the main feeding teeth are always correlated with the shape of the central rachidian tooth (personal observation). The central tooth is the easiest to mount in a consistent orientation, so it was used as the primary tooth to determine tooth shape. Only teeth on the youngest half of the radula were examined. No teeth that had been used for feeding (the first five to six rows) were used to determine tooth shape.

RESULTS

All *Lacuna vincta* and *L. variegata* fed epiphytes on eelgrass and kept in a tank containing eelgrass produced blunt teeth (Table 1; Figure 1). Similarly, all *L. vincta* and *L. variegata* fed kelp and kept in a tank containing kelp produced pointed teeth (Table 1; Figure 1). No intermediate-shaped teeth were found in any individuals. Within each treatment, no differences were found as a function of size or sex of snails. The results of a 3-way G test showed that for both *L. vincta* and *L. variegata*, food had a significant effect on tooth from ($P < 0.001$), and the two species did not differ in this respect.

DISCUSSION

Although radular morphology is generally considered stereotypic within species, and is frequently used as a taxonomic character and for species identification (Fretter & Graham, 1994), I found that radular morphology is plastic for both of these species (Table 1). Animals fed kelp and kept in a kelp environment produced pointed teeth, whereas those fed epiphytes and kept in an eelgrass environment produced blunt teeth (Figure 1). Radular variability within gastropod species is often considered anomalous or unexplained (Howe, 1930; Langan, 1984; Reid, 1988, 1996). In *Peristernia*, tooth number and cusp length vary greatly among and within rows of teeth, and may be an extreme case of fluctuating asymmetry (Taylor & Lewis, 1995). In some cases, tooth shape may change ontogenetically (Nybakken, 1990), or tooth size may be different for animals found on different host plants (Bleakney, 1990). Variation in radular tooth form in species of *Lacuna* has caused some question in regard to species identifications (King, 1965; Langan, 1984; Langan-Cranford & Pearse, 1995). This is the first demonstration that radular tooth form can be phenotypically plastic and inducible in adult snails.

The inducible plasticity of the *Lacuna* radula is remarkable, not only because it occurs in what is traditionally thought of as a species-specific character, but also because this is the first case of non use-induced plasticity in a feeding structure for any invertebrate. Plasticity in the feeding apparatus has been demonstrated in a wide array of taxa including fishes, insects, arachnids, and crabs (Bernays, 1986; Meyer, 1987; Wimberger, 1991; Thompson, 1992; Smith & Palmer, 1994). In all of the previous studies, the mechanical use of the apparatus controls the remodeling of the structure. The nature of the morphogenesis of the radula precludes this type of remodeling. Once a tooth has developed, its morphology cannot be changed. Instead, the induced morphology is found only on new teeth produced in the new environment, physically distant from the teeth in use. The morphological induction seen in *Lacuna* is much more similar to that seen in anti-predator induced morphologies such as in bryozoans (Harvell, 1990).

Although variability in radular morphology frequently has been viewed as anomalous, if inducible morphological plasticity is heritable, it is the raw material on which natural selection will act, and could be adaptive (Stearns, 1989; West-Eberhard, 1989; Thompson, 1991; Padilla & Adolph, 1996). The fact that radular morphology can be phenotypically plastic is a major finding, and has impor-

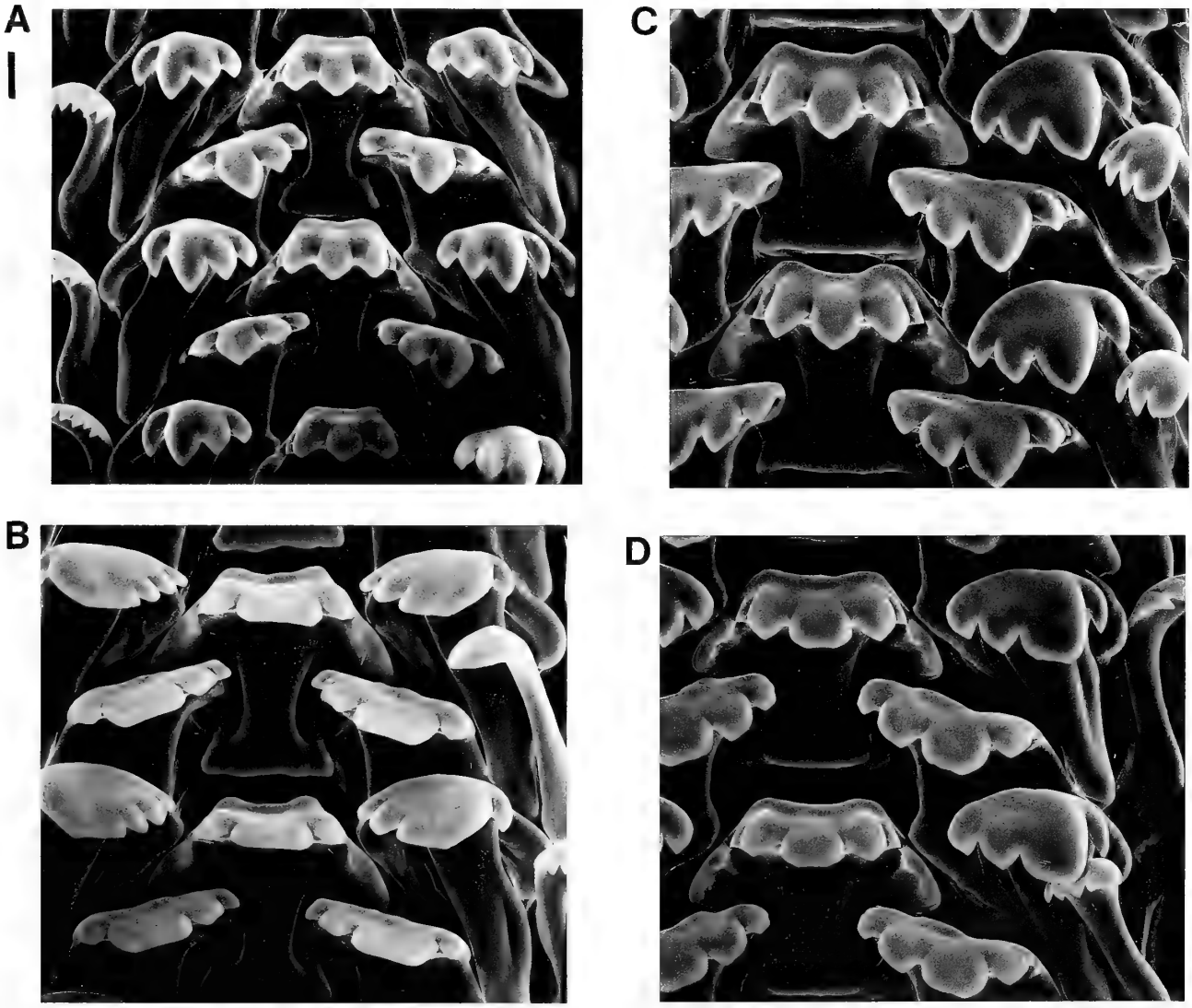

Figure 1

Scanning electron micrographs of the radulae of *Lacuna variegata* (A, B) and *L. vincta* (C, D). Animals held in a kelp bed environment and fed kelp produced pointed teeth (A, C), whereas those held in an eelgrass environment and fed epiphytes produced blunt teeth (B, D). Scale bar = 10 μm.

tant implications not only for ecology, but for molluscan taxonomy and systematics. Clearly radular tooth shape can be a labile trait and sensitive to natural selection. Using radular form for taxonomic and systematic purposes therefore must be approached with caution. Ecologically, we might expect other species living in highly variable habitats in which different morphologies have advantage to display similar plasticities. If a species occurs in a wide range of habitats, moves from habitat to habitat, or if habitat conditions change during the lifetime of an individual, a single optimal phenotype may not exist. For species of *Lacuna* in the northeastern Pacific, pelagic larval dispersal of 4 to 12 weeks is common, and juveniles and adults regularly move among habitats by drifting on mucus threads (Martel & Chia, 1991b, c). Therefore, individuals with a fixed phenotype may be at a disadvantage, and the ability of individuals to change their phenotype to best take advantage of current environmental conditions could be adaptive (Padilla & Adolph, 1996). Many gastropods, especially those in the intertidal and shallow subtidal zones, may be subject to such environmental changes. Other species of *Lacuna* have been found to have variable radular tooth morphologies similar to those studied here (Langan, 1984; Langan-Cranford & Pearse 1995), and six of 19 species of *Littorina* show intraspecific radular shape variability par-

alleling that seen in *Lacuna* (Padilla & Dittman, unpublished data). By examining more species where unexplained intraspecific variability has been noted, we may find many more examples of phenotypically plastic inducible radular morphologies.

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NOTES, INFORMATION & NEWS

Distinguishing the Dark Falsemussel, *Mytilopsis leucophaeata* (Conrad, 1831), from the Non-Indigenous Zebra and Quagga Mussels, *Dreissena* spp., Using Spermatozoan External Morphology

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Introduction

The bivalve family Dreissenidae is composed of the two extant genera *Mytilopsis* (Conrad, 1857) and *Dreissena* (van Beneden, 1835). Worldwide, there are nine species of *Mytilopsis* inhabiting tropical and temperate brackish habitats. Two of these are found in estuaries in the temperate and subtropical western Atlantic. The dark falsemussel, *Mytilopsis leucophaeata* (Conrad, 1831), inhabits brackish waters from the Hudson River to Tampico, Mexico (Abbott, 1974), whereas *Mytilopsis sallei* (Récluz, 1849) occurs in similar habitats from southern Florida through the Gulf of Mexico and the Caribbean (Marelli & Gray, 1983).

Until recently, the only members of the family Dreissenidae which occurred in North America were those of the genus *Mytilopsis*. In the mid 1980s, however, the zebra mussel, *Dreissena polymorpha* (Pallas, 1771) was introduced into the Great Lakes region from Europe, most probably via the release of veliger larvae in ballast water of trans-Atlantic ships (Hebert et al., 1989). Shortly thereafter, the quagga mussel, *Dreissena bugensis* (Andrusov, 1897), was introduced in the same manner, apparently into Lake Ontario (May & Marsden, 1992). Both species are now serious biofoulers in North American waters.

Since the introduction and spread of *Dreissena polymorpha* and *D. bugensis* in North America, areas of overlap between the ranges of these two species and *Mytilopsis leucophaeata* have occurred, and have at times led to confusion regarding differentiation among these species (O'Neill, 1990). Pathy & Mackie (1993) compared the internal and external morphology, ultrastructure, and composition of the shells of these three dreissenid mussels, and found clear distinctions among them. These distinguishing characteristics include the presence of an internal apophysis or shelf within the shell of *Mytilopsis*, the ventrolateral shell carina of *D. polymorpha*, and the relative amounts of microtubules present in the ultrastructure of shells of the three species. However, in some circumstances (e.g., damaged shells, older eroded shells, and shells which have an abnormal shape due to physical limitations on growth), identification of the dreissenid mussel species in question based solely on shell morphology might not be conclusive. An additional means of comparing the different species therefore would be useful in increasing the certainty of identification.

Denson & Wang (1994) and Walker et al. (1996) described differences in the morphology of the spermatozoa of *Dreissena polymorpha* and *D. bugensis* that are useful for differentiating between those two species. Spermatozoa morphology has been found to have taxonomic significance within a number of other taxa as well (Hodgson & Bernard, 1988; Popham, 1974, 1979; Jamieson et al., 1991; Franzen, 1992; and Healy, 1996). The present study describes the external morphology of *Mytilopsis leucophaeata* sperm and identifies characteristics that are useful in differentiating among all three species.

Materials and Methods

Mytilopsis leucophaeata were collected on 12 March 1994 from the upper Davis Bayou near Ocean Springs, Mississippi (30°24′2.4″N, 88°45′26.3″W). *Dreissena polymorpha* and *D. bugensis* were collected on 22 July 1993 from the Black Rock Lock adjacent to the Niagara River in Buffalo, New York (42°55′52.3″N, 78°54′7.1″W). After examining a squash preparation of a small portion of the visceral mass using light microscopy, gonadal tissues found to contain spermatozoa were fixed in glutaraldehyde (diluted to 2.5% in 0.1 M cacodylic acid buffer, pH 7.2) for 2 hours. The glutaraldehyde was removed by three sequential 5 min washes in the same buffer solution. Afterward, the samples were dehydrated through the following series of ethanol solutions: 25%, 50%, 70%, 90%, 100% (3×). To remove all liquid, tissues were desiccated in a critical point dryer using liquid CO_2. They were then mounted on aluminum stubs and coated with a thin (approximately 40 Å) film of gold in an argon atmosphere. The coated tissues were then examined using an Electroscan environmental scanning electron microscope and the spermatozoa photographed.

Results

The general shape of the head portion of the *Mytilopsis leucophaeata* sperm, exclusive of the acrosome and mi-

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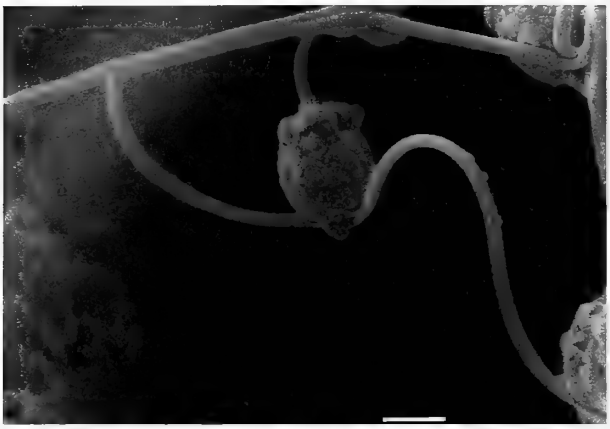

Figure 1

Scanning electron photomicrograph of the spermatozoa of *Mytilopsis leucophaeata.* Scale = 1 μm.

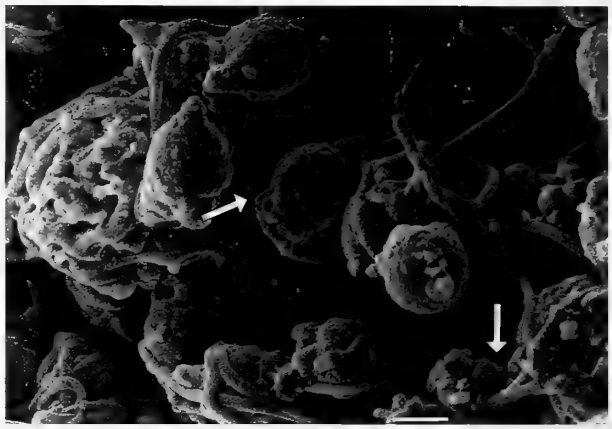

Figure 2

Scanning electron photomicrograph of the spermatozoa of *Mytilopsis leucophaeata* showing the off-centered insertion of flagellum and chondriome assembly of three mitochondrial sacs (arrows). Scale = 1 μm.

tochondrial sacs, is broadly rounded, appearing relatively spherical (Figure 1). Including the acrosome and chondriome, the mean length and width of the head are 2.3 ± 0.2 μm and 1.5 ± 0.03 μm, respectively (n = 10). Each sperm head appears to bear three mitochondrial sacs at the point of flagellum insertion. The flagellum is attached to the sperm head in an off-centered, nearly lateral position (Figure 2). It is approximately one-sixth the width and roughly 15 to 20 times the length of the head portion.

There are distinct differences in external morphology among the spermatozoa of *Mytilopsis leucophaeata, Dreissena polymorpha*, and *D. bugensis*. The heads of the spermatozoa of both *Dreissena* species are elongated and tapered, with conical rather than spherical outlines, as compared to the roundness observed in *Mytilopsis* in this study (Figure 3). In the zebra and quagga mussel sperms, the tapering of the acrosome approximates that of the main portion of the sperm head, and the acrosome shows no apparent external segmentation. In contrast, the acrosome of *Mytilopsis* sperm is dwarfed by the globular head portion. It is distinctly bilobate, with a taller, wider proximal portion and a shorter, narrower distal portion which tapers to a rather blunt apex. The heads of *Mytilopsis* sperm are about the same width as those of zebra and quagga mussels, but substantially shorter.

In the quagga and zebra mussel sperm, the chondriome is composed of four mitochondrial sacs. In those of *Mytilopsis*, however, only three such structures are evident. Among the *Dreissena* species, the flagellum is inserted into the sperm head at the center of its base, and is encircled by the four large mitochondrial sacs. By contrast, the insertion of the flagellum is off-centered in the sperm of *M. leucophaeata,* being adjacent to, rather than surrounded by, the chondriome assembly.

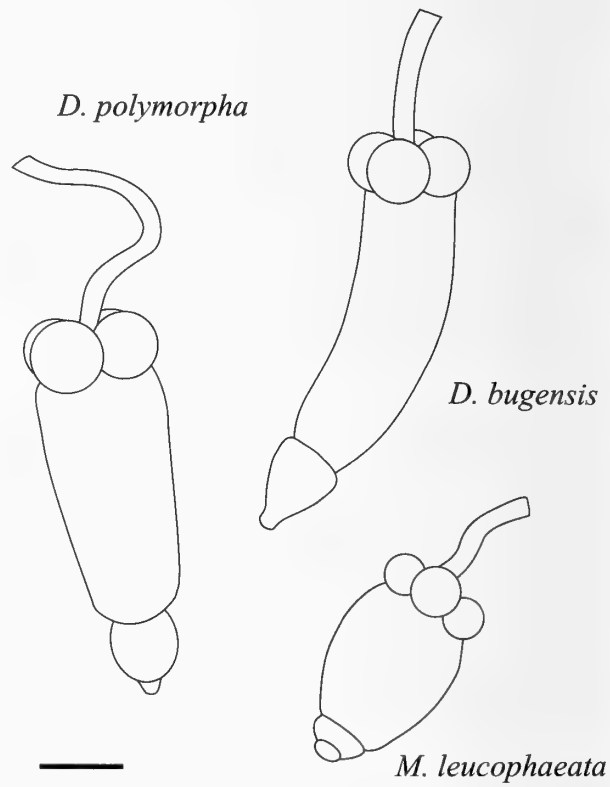

Figure 3

Comparison of the spermatozoan external morphology of *Dreissena polymorpha, D. bugensis*, and *Mytilopsis leucophaeata.* Only a portion of the flagellum of each is shown. Scale = 1 μm.

Discussion

The type of spermatozoa found in the bivalve species discussed here is not unique to dressenid mussels. It has been noted in at least 13 invertebrate phyla, and is characterized by a short round or conical head, several large structures containing mitochondria which are collectively termed the chondriome (Dohmen, 1983), and an acrosome at the tip of the head portion. Spermatozoa of this morphological construction are normally ectaquasperm i.e., those which unite with ova in the water outside the body (Rouse & Jamieson, 1987) as is the case with dreissenid mussels.

The differences in spermatozoa morphology described may serve as one means of discriminating among males of *Mytilopsis leucophaeata, Dreissena polymorpha*, and *D. bugensis*. The differences are quite distinct and can be observed using a light microscope. Examining simple squash preparations at 400 or 1000× magnification, we have been able to discriminate among the broadly ovate sperm of *Mytilopsis leucophaeata*, the straight, conical sperm of *Dreissena polymorpha*, and the curved, more pointed sperm of *D. bugensis*. Results from the present study serve to reinforce the concept of the usefulness of microscopic and submicroscopic evaluations of sperm morphology as systematic and taxonomic tools.

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Observations on the Reproduction of *Bifurcium bicanaliferum* (Sowerby, 1832) (Gastropoda: Columbellidae: *Strombina*-group) from the Pacific Coast of Panama

Helena Fortunato[1], Pablo E. Penchaszadeh[2] and Patricia Miloslavich[3]

Introduction

The *Strombina*-group sensu Jung, 1989, is an exclusively tropical American group represented by more than 30 living species in the Eastern Pacific, but by only four in the Caribbean, where it suffered massive extinction at the end of the Pliocene. The reproductive patterns are known for only two Caribbean species (Cipriani & Penchaszadeh, 1993), both with direct development. For Pacific species there is only indirect evidence of larval development based on the size and number of whorls of the larval shell (Jung 1986, 1989; Jackson et al., 1996).

Bifurcium bicanaliferum (Sowerby, 1832) is an Eastern Pacific member of the *Strombina*-group which is the only living species of a genus otherwise known from Miocene deposits of the Caribbean. The following is the first description of some aspects of the reproduction of this species.

Materials and Methods

Living adults of *Bifurcium bicanaliferum* were collected during the dry season (January through March) of 1994 and 1995, at Playa Bique, a small muddy beach on the Pacific coast of Panama, about 30 km NW of Panama City, near the village of Veracruz. Specimens were found both buried in the mud and crawling on the surface. The sampling area consisted of a small beach with a surface layer of thick, black, organic mud about 30 cm deep overlying a hard bottom. The beach is exposed at extreme low tides during the upwelling season from December to April.

Specimens with eggs constituted about 10% of the total number of living animals found during the collecting season. More than 100 animals with compact masses of egg capsules attached to the shell were collected selectively, brought to the marine laboratory of the Smithsonian Tropical Research Institute in Naos island, near Panama City, and maintained in an aquarium with aerated seawater. The egg capsules were examined and the eggs and embryos counted and measured; statistics are given as mean ± 1 standard deviation. Protoconch volution measurements follow Jung (1989). Measurements were made with a WILD M7 stereoscopic microscope at 25×. A Scanning Electron Microscope JEOL 5300LV was used to photograph veliger shells and egg capsules, which were cleaned with filtered seawater and kept in a 70% ethanol solution before being coated with gold. Adult specimens, egg capsules, and veliger shells of *Bifurcium bicanaliferum* were deposited at the Field Museum of Natural History (FMNH), Chicago.

Results and Discussion

The shells were covered almost entirely by egg capsules (Figure 1). Most shells presented successive compact layers of egg capsules.

Capsules were translucent, yellow, and hemispheric, with a slightly concave basal wall. A narrow, thin, and irregular flange surrounded the egg capsule. The escape aperture, covered by a thin membrane, is almost circular and situated in the center of the egg capsule (Figures 2, 3).

Most of the egg masses examined had egg capsules in different stages of development. Many of the egg capsules in the inner layer contained dead embryos. The average number of eggs per egg capsule was 22 ± 2 (n = 24) eggs. These were round, yellow, and measured 152 ± 12 microns (n = 30) in diameter.

Development passed through a trochophore stage with two velar lobes. The pre-hatching, intracapsular veliger measured 163 ± 12 microns (n = 9) in shell length. The average number of hatchlings per capsule was 20 ± 3 (n = 29). The shell was transparent, without any pigmentation, very fragile, and with no siphonal canal.

The hatching stage was characterized by a veliger with 1.5 whorls measuring 234 ± 10 microns (n = 40) in length. The shell was transparent with a short siphonal canal and a reddish edge (Figure 4). The shell was starting to calcify as shown by the lines of deposition on the micro photograph. The veliger had a large bilobate velum with black spots at the base of the velar cilia and a round operculum. The hepatopancreas, stomach, anus, branchia, and heart were all visible through the shell. Intracapsular veligers increased their movement the day prior to hatching and were very active at hatching, searching for light and remaining near the surface of the water. They survived as swimming larvae for at least 10 days in aquarium conditions.

Although egg laying was not witnessed, the fact that no other gastropods were found in the area at the time of our collections, and that the same kind of egg capsules was found in consecutive years associated with this species leads us to conclude that these egg capsules belong to *Bifurcium bicanaliferum*. Jung (1989:60, fig. 82, pls. 19–21) reported the finding of dried egg capsules attached to several shells of *Strombina lanceolata* (G. B.

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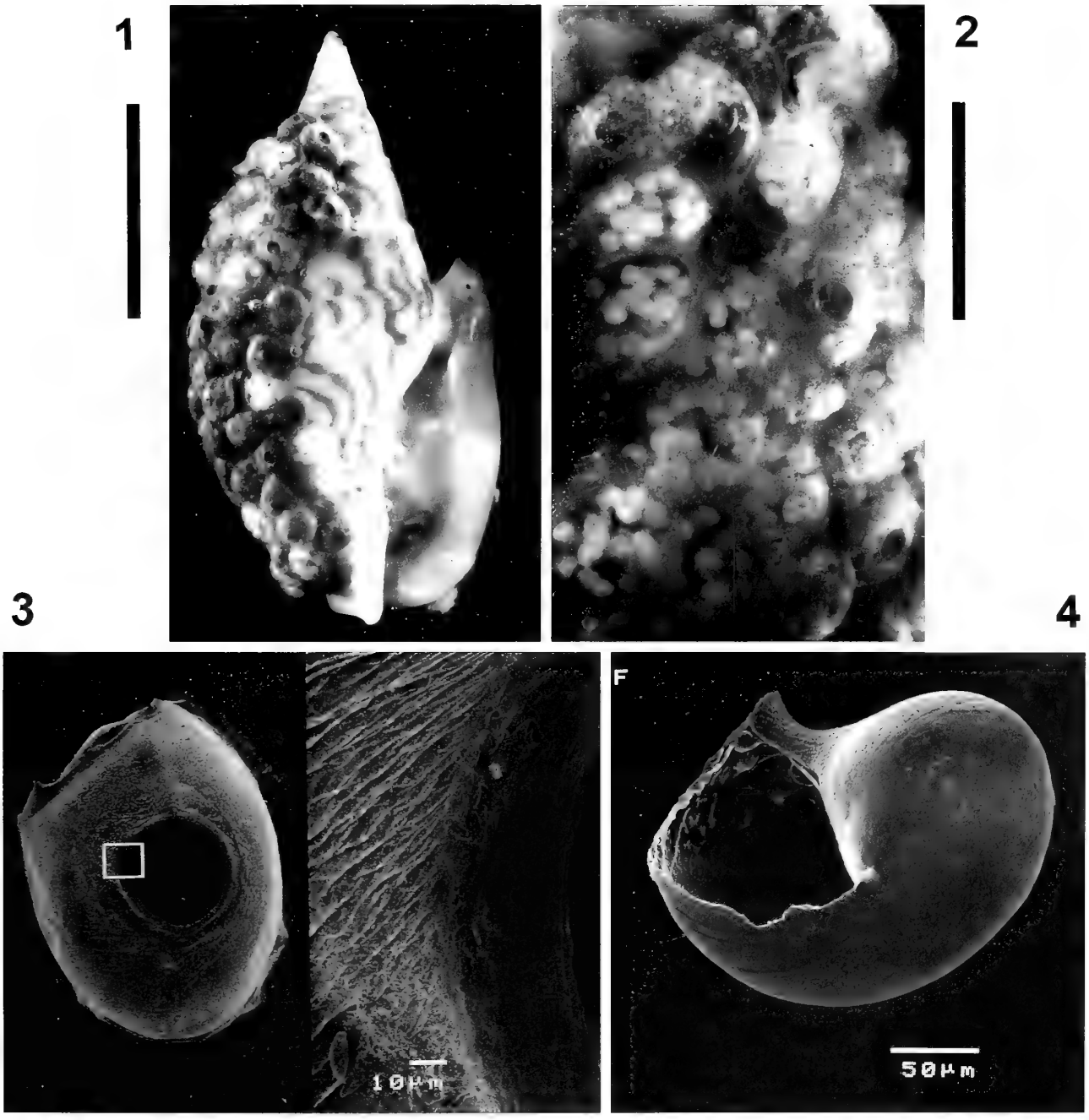

Explanation of Figures 1 to 4

Figure 1. *Bifurcium bicanaliferum* (FMNH 293337) from the Pacific coast of Panama, with egg capsules attached to the shell. Scale bar = 5 mm; Figure 2. Egg capsules of *Bifurcium bicanaliferum*. Scale bar = 2 mm; Figure 3. SEM picture of the top view of an empty capsule of *Bifurcium bicanaliferum*; Figure 4. SEM picture of the hatching veliger shell of *Bifurcium bicanaliferum*.

Sowerby, 1832) from the Galapagos Islands. A similar egg-laying strategy has also been observed in other species of the *Strombina*-group (Fortunato, in preparation), and was reported for two Caribbean *Strombina* species (Cipriani & Penchaszadeh, 1993).

The reproductive pattern of *Bifurcium bicanaliferum* is very different from the Caribbean species belonging to the *Strombina*-group studied earlier (Table 1) (Cipriani & Penchaszadeh, 1993).

The egg capsule masses of *B. bicanaliferum* usually

Table 1

Summary of reproductive aspects for three species of the *Strombina* group. Statistics are mean ± 1 standard deviation.

	Bifurcium bicanaliferum	*Strombina francesae**	*Strombina pumilio**
Egg capsule length (mm)	1.0 ± 0.1 (n = 27)	2.4 ± 0.3	2.1–2.4
Egg capsule width (mm)	0.8 ± 0.1 (n = 27)	2.1 ± 0.2	2.0–2.1
Egg capsule aperture length (mm)	0.3 ± 0.01 (n = 27)	1.3 ± 0.3	1.3
Egg capsule aperture width (mm)	0.2 ± 0.02 (n = 27)	0.9 ± 0.1	1.0–1.1
Eggs/capsule	22 ± 2 (n = 24)	5	5
Egg diameter (μm)	151 ± 11 (n = 30)	571 ± 35 (n = 22)	616 ± 48
Embryos/egg capsule	20 ± 3 (n = 29)	5	5
Shell length at hatching (μm)	234 ± 10 (n = 40)	900 ± 46	947 ± 97
Hatching stage	veliger 1.5 whorls	crawling juvenile 1.25–1.5 whorls	crawling juvenile 1.25–1.5 whorls
Extra food resources for the embryo	no evidence of nurse eggs; probable later stage cannibalism	no evidence of nurse eggs or cannibalism	no evidence of nurse eggs or cannibalism

* Data from Cipriani & Penchaszadeh, 1993.

have several layers, whereas both *Strombina pumilio* and *S. francesae* have only one layer of egg capsules attached to the adult shell. Moreover, egg capsules of the Eastern Pacific species are also much smaller than those of the Caribbean species and contain more than 4 times the number of eggs.

The egg diameter of *Bifurcium bicanaliferum* is among the smallest in the Columbellidae (151 microns) (Amio, 1957, 1963; d'Asaro, 1970; Bandel, 1974), whereas the egg diameters of both *Strombina pumilio* and *S. francesae* are the largest recorded in the family (616 and 571 microns, respectively). In none of these species is there evidence of nurse eggs. On the other hand, some egg capsules of *Bifurcium* contained several empty veliger shells prior to hatching, suggesting the possibility of some sort of late intracapsular cannibalism.

Bifurcium bicanaliferum hatches as veliger larvae, whereas both Caribbean *Strombina* species hatch as crawling juveniles. These differences are reflected in both the size and the morphology of their larval shells. The larval shell of the *Strombina* species studied earlier is 4 times greater (900 and 940 microns) than the hatching veliger shell of *Bifurcium*. The number of protoconch whorls is the same (1.25–1.5) in both the juveniles and the adults of *Strombina pumilio* and *S. francesae*, whereas the hatching veliger of *Bifurcium bicanaliferum* only has 1.5 whorls. However, the protoconch of the adult *B. bicanaliferum* consists of 2.5 volutions, which strongly suggests that *Bifurcium* larvae spend considerable time in the plankton before settling. Planktonic development was not observed because all the veligers died within 2 weeks after hatching. At this time the veliger shell had 1.7 whorls.

Acknowledgments

We thank Anibal Velarde, Javier Jara, and Marcos Alvarez for their help in the field. Jorge Ceballos helped with the SEM photographs. Jeremy Jackson, Roberto Cipriani, and two anonymous reviewers criticized the manuscript and made many helpful suggestions. This work was supported by the Smithsonian Tropical Research Institute Naos Marine Laboratory, by a grant of the Swiss Science Foundation, by a subvention from the Decanato de Investigaciones of the Universidad Simón Bolivar, and from the Fundación Antorchas, Argentina.

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International Commission on Zoological Nomenclature

The following Application was published on 30 September 1997 in Volume 54, Part 3 of the *Bulletin of Zoological Nomenclature*. Comment or advice on this application is invited for publication in the *Bulletin* and should be sent to the Executive Secretary, I.C.Z.N., c/o The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

Case 3013—*Helix draparnaudi* Beck, 1837 (currently *Oxychilus draparnaudi*; Mollusca, Gastropoda): proposed conservation of the specific name.

The following Opinions concerning mollusks were published on 30 September 1997 in Volume 54, Part 3 of the *Bulletin of Zoological Nomenclature*. Copies of these Opinions can be obtained free of charge from the Executive Secretary at the address given above.

Opinion 1877. D. L. G. Karsten (1789), *Museum Leskeanum*, vol. 1 (Regnum Animale): suppressed for nomenclatural purposes.

Opinion 1880. Plutoniinae Bollman, 1893 (Arthropoda, Chilopoda): spelling emended to Plutoniuminae, so removing the homonymy with Plutoniinae Cockerell, 1893 (Mollusca, Gastropoda).

The Veliger 41(2):212 (April 1, 1998)

THE VELIGER

BOOKS, PERIODICALS & PAMPHLETS

Response to Review by B. Roth of "*Guamampa* n.g. (Gastropoda, Pulmonata), a Land Snail with Monadeniid Characters," Volume 40(4):368–370

As a rule, I prefer to discuss some professional problems with colleagues personally before publication of an article, and I usually refrain from public polemics. Dr. Roth and I had a chance to discuss general approaches to the problem of phylogeny a few years ago, but at that time we did not achieve agreement. It seems to me that this time we also will stay on our former positions.

In the text of the review there are a number of questions I would not like to discuss here (I do not understand why I may not compare two species, *Aegista subchinensis* and *A. chinensis*; why in a *schematic* sketch of phylogenetic trees I must put in *all* the diversity of side branches); but I would like to consider briefly some principal points.

In essence, the criticism by Dr. Roth is not a criticism of the given paper and not a criticism of my article of 1991. It is a criticism of the approach to phylogenetic problems which the reviewer characterizes as "conjectural, non-analytical, and authoritarian." The same words could be applied to the phylogenetic constructions suggested by H. A. Pilsbry, H. B. Baker, J. Thiele, A. Solem, and many other authors who did not use cladistic methods.

I have given an account of the principles of my approach on pp. 187–188 of my 1991 article and there is no necessity to repeat them. I would simply like to stress that the main basis of my phylogenetic conclusions is morpho-functional analysis of particular systems, apparatus, and organs. Dr. Roth reproaches me for using (in my paper of 1991) only characters of the lower reproductive tract. Indeed, in helicoid groups, that is the most informative part. If I were analyzing, for example, the Clausiliidae, I would use mainly the closing apparatus in the aperture, etc.

Dr. Roth prefers the cladistic method. Okay, why not, but I am decidedly against the proclamation of cladistics as the only scientific method. To my mind, cladistics has its own shortcomings, chief among them the formalistic (and non-analytical) incorporation in the analysis of all available features without preliminary weighting from the point of view of their functions. I could not agree more with Dr. Roth that "cladistic analysis . . . presents problems of its own," and not only in the paper under consideration.

Finally, I would like to add that the style of the critique unfortunately is not less authoritarian than, in Dr. Roth's opinion, my taxonomic and phylogenetic conclusions.

A. Schileyko

Bulletin of the Russian Far East Malacological Society, Vol. 1.

A new molluscan serial has appeared on the scene. Published in Vladivostok, volume 1, dated "1996," was, according to a penned note, actually issued on April 20, 1997. It has 91 pages and six articles: A. I. Kafanov & K. Amano, Japanese contribution to the Cenozoic marine bivalve paleontology of Sakhalin and Kurile Islands; L. A. Prozorova, Gastropods and small bivalves of fresh and brackish waterbodies of the southern Kurile Islands. Annotated list of species; L. A. Prozorova, Genus *Conventus* (Bivalvia, Pisidioidea) from the Russian Far East; G. A. Evseev, Bivalve molluscs from shelf deposits of East Korean Bay, the Sea of Japan; A. I. Kafanov, *Corbicula zhidkovae* nom. nov.—replacement for *Corbicula convexa* Zhidkova in Arkhipova et al. [1994] *non* Deshayes, 1855; Yu. M. Yakolev & N. K. Kolotukhina, The reproduction of the molluscs *Cryptonatica janthostoma* (Deshayes, 1841) and *Lunatia pila* (Pilsbry, 1911) (Gastropoda, Naticidae) in the Sea of Japan. The issue also contains useful bibliographies for some of the society's founding members, including George A. Evseev, Vladimir V. Gulbin, Alexander I. Kafanov, Konstantin A. Lutaenko, Larisa A. Prozorova, Amelie H. Scheltema, and Yuri M. Yakovlev, and an essay, Current state of malacological research in the Russian Far East, by A. I. Kafanov & K. A. Lutaenko. Two of the articles are in English with Russian abstracts; the other four are in Russian with English abstracts.

The Editor is Alexander I. Kafanov, Institute of Marine Biology, 17 Palchevsky St., Vladivostok, Russia 690041. Subscriptions come with membership, which can be obtained for $5 [$2.50 for students] by applying to the Secretary: Konstantin A. Lutaenko, at the same address.

E. V. Coan

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References in the text should be given by the name of the author(s) followed by the date of publication: for one author (Phillips, 1981), for two authors (Phillips & Smith, 1982), and for more than two (Phillips et al., 1983). The reference need not be cited when author and date are given only as authority for a taxonomic name.

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Hickman, C. S. 1992. Reproduction and development of trochacean gastropods. The Veliger 35:245–272.

b) Books:

Bequaert, J. C. & W. B. Miller. 1973. The Mollusks of the Arid Southwest. University of Arizona Press: Tucson. xvi + 271 pp.

c) Composite works:

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117–135 in R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), Intertidal Invertebrates of California. Stanford University Press: Stanford, Calif.

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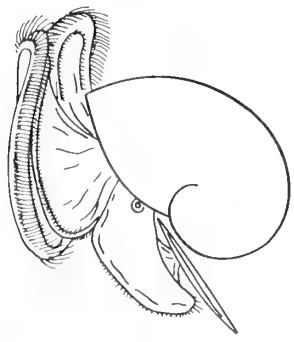

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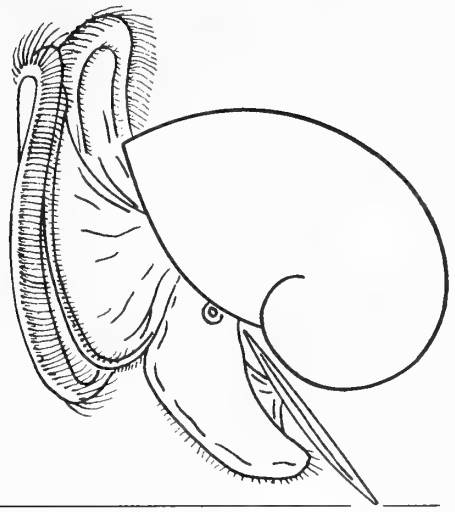

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CONTENTS — *Continued*

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The Veliger 41(3):213–226 (July 1, 1998)

THE VELIGER

The Feeding Habits of *Pleurobranchaea californica* MacFarland, 1966 (Opisthobranchia: Notaspidea) in Monterey Bay, California

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Abstract. The natural diet of *Pleurobranchaea californica* was studied in Monterey Bay, California. Specimens were collected from 29 January to 9 November 1992, at depths of 30–100 m using an otter trawl and an interfacial trawl. Three hundred fifty-six individuals were collected and ranged in size from 0.01–411 g with most of the individuals weighing between 1.0 and 50 g. The gut contents were examined and 16 different taxa were identified. Thirty-three percent of the guts were empty. Many animals had sediment in their guts, which was presumed to be a result of their ingesting or attempting to ingest prey. *Pleurobranchaea californica* was found to be a euryphagic predator with pronounced cannibalism. Individual Index of Relative Importance values showed that opisthobranchs made up the largest portion of the diet. The opisthobranchs in the diet included *Pleurobranchaea californica* (as prey), *Armina californica,* and *Aglaja* sp. The diets were similar for specimens of *P. californica* collected at all depths, but did change depending upon the season in which the animals were collected.

INTRODUCTION

The natural history and feeding habits of most notaspideans are not well known. Cattaneo-Vietti et al. (1993) suggested that the research on notaspideans is limited because it is difficult to obtain a sufficient number of specimens. Willan (1984), in an overview of notaspidean diets, reported that the majority of observations on food and feeding in the literature were from incidental reportings in otherwise taxonomic studies.

Pleurobranchaea californica MacFarland, 1966, is the largest and most abundant notaspidean found off the coast of central California in depths from 10–400 m (Coan, 1964; Chivers, 1967; Behrens, 1991). It ranges in length from 8–210 mm (MacFarland, 1966; Chivers, 1967; Behrens, 1991).

Pleurobranchaea californica has been used extensively as an experimental animal in neurophysiological research (Davis et al., 1977; Ram & Davis, 1977; Gillette & Davis, 1977; McClellan, 1982) and in avoidance conditioning experiments (Mpitsos & Davis, 1973; Mpitsos & Collins, 1975; Davis et al., 1980), but little work has actually been done on its natural history. The only studies, relative to diet, that have been done on *P. californica* are some laboratory observations of feeding behavior (Coan, 1964; Chivers, 1967; Lee et al., 1974; Morse, 1984) and an anatomical study of its digestive system (Morse, 1984).

Observations of feeding behavior in captivity and morphology of the digestive system led Morse (1984) to suggest that *P. californica* is carnivorous and can probably ingest large prey. Morse (1984) found that one specimen of *P. californica* had ingested an entire opisthobranch of the genus *Berthella.* Chivers (1967) also found *P. californica* to be carnivorous in captivity, eating whatever organisms were supplied, including the anemone *Anthopleura elegantissima* and other specimens of *P. californica,* but the question of the food of *P. californica* in nature remained unanswered.

The primary goal of this study was to establish the natural diet of *P. californica* in Monterey Bay, California. Ancillary goals were to determine whether the diet of *P. californica* differed with depth, season, and the size of the *P. californica.*

MATERIALS AND METHODS

Specimens of *Pleurobranchaea californica* were collected weekly in Monterey Bay, California from 29 January 1992 to 9 November 1992. Inclement weather conditions precluded collecting specimens in December, and in January and February specimens were only collected one day out of each month.

The collections were made in three separate areas in Monterey Bay (Figure 1). Area A, an extensive area located north of the Monterey Canyon and east of Soquel Canyon, had muddy bottom sediments with very little debris and was the most favorable area for finding *P. californica.* Area B, located south of Area A and Monterey Canyon, had more coarse sandy sediment than the other areas, and drift kelp and debris were common on the bottom. Very few or no individuals of *P. californica* were caught in this area. Area C, located northwest of Area A and Soquel Canyon, and directly south of Santa

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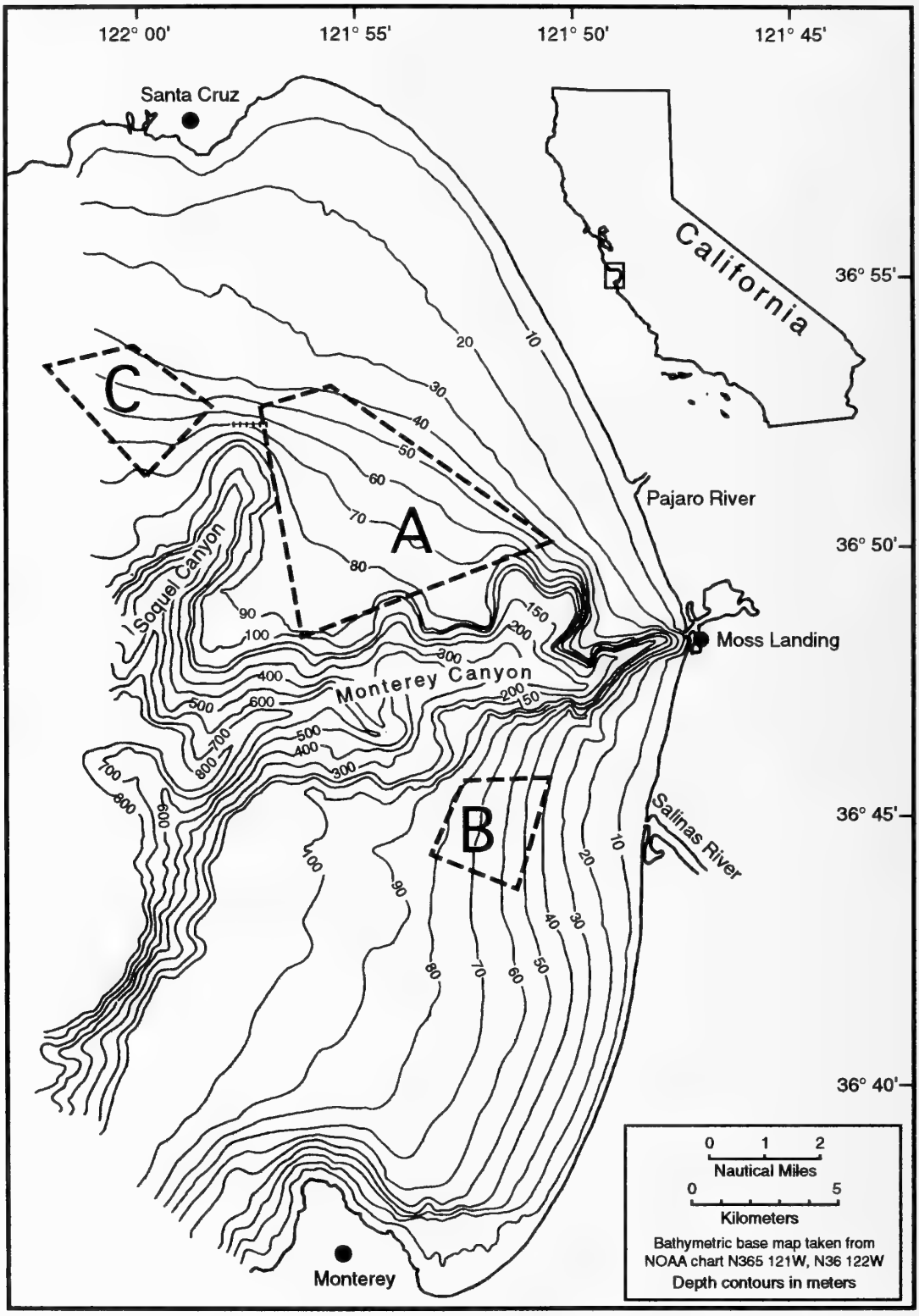

Figure 1

Map of Monterey Bay. Dashed lines enclose the trawled areas.

Table 1

Number and type of trawls used per month and the number of days trawled per month

Month	Otter trawl	Interfacial trawl	Days
January	8	0	1
February	8	0	1
March	18	0	3
April	21	0	4
May	16	0	4
June	12	0	3
July	16	0	3
August	6	0	1
September	6	5	3
October	9	5	3
November	8*	1	2
December	0	0	0
Total	128	11	28

* Four day trawls and 4 night trawls.

Cruz, was similar to Area A, but was infrequently trawled because of greater travel time from Moss Landing.

Specimens of *P. californica* were collected from the R/V *Ed Ricketts,* a 10.7 m research vessel, using a 7.2 m otter trawl and a 0.8 m interfacial trawl. The interfacial trawl was used to collect the smallest specimens of *P. californica* that would normally be expected to pass through nets of otter trawls. However, in practice we found that the otter trawl actually brought up more small specimens of *P. californica.* These small specimens of *P. californica* were found clinging to the net and on the deck of the boat when the net was retrieved. The otter trawl sampled a larger bottom area of approximately 7931 m^2 per trawl, while the interfacial trawl covered approximately 245 m^2 per trawl. The larger area of coverage meant that the otter trawl collected more specimens of *P. californica.*

The time, location, and bottom depth were recorded for each trawl. A total of 139 trawls was done. There were 124 daytime otter trawls and four taken at night (Table 1). The remaining 11 trawls were interfacial (Table 1). The trawling time was the time, in minutes, from when the trawl was placed in the water until it was brought back on board. The times for otter trawls ranged from 12–25 min and for the interfacial trawl 10–12 min. The depths trawled ranged from 34–100 m.

The interfacial trawl, unlike the otter trawl, brought up considerable mud with the animals. The mud was removed from the trawl and filtered through a 2 mm mesh screen to retrieve the specimens. The superstructure of the sled was also examined for any specimens of *P. californica* clinging to it.

Individuals of *P. californica* were washed free of debris, their guts were injected with 1–2 mm of 10% formalin to stop digestion, and placed separately into marked Ziploc bags and set aside. The same day, the animals were each transferred from the bag into a jar of 10% formalin, where they were kept until the time of dissection.

Each large specimen was weighed to the nearest 0.1 g and the smallest to the nearest 0.01 g. After the animals were removed from the storage bottle, the formalin was filtered through a 1 mm screen for any prey that might have been regurgitated. The entire gut, including the buccal mass, esophagus, crop, and stomach, was removed from the body and examined for prey.

The esophagus, crop, and stomach were cut open longitudinally and the percent fullness (%F) and state of digestion were subjectively determined. When the entire gut was full and enlarged (by observation only, no repeatability tests were made), it was considered to be 100% full. If the gut was just full but not enlarged, it was recorded as 90% full. The other percent fullness amounts corresponded to how much of the gut was filled with material. The state of digestion was scored by a process similar to that of Ambrose (1976) and Tyler (1970), as: 1 = advanced digestion, nothing recognizable; 2 = medium digestion, mostly digested material but with some animal parts recognizable; 3 = early digestion, some digested material, some undigested animals; and 4 = no digestion, undigested whole animals.

Prey removed from the gut were identified to the lowest possible taxon and measured, when possible, to the nearest 0.1 mm with an ocular micrometer on a dissecting microscope. Because the gut contents often had many different prey types in different stages of digestion along with large amounts of sediment, which made it impractical to directly measure volume, the percent volume contribution of each prey type to the total percent volume was estimated by eye (Bray & Ebeling, 1975). There is a subjective bias estimating volume by eye, but Bray & Ebeling (1975) reported that an observer's overestimation of volume on one trial was often countered by an underestimation of the same volume on the next trial thus minimizing the bias. In this study, the bias was minimized by making trial estimations of volume, on gut contents, before the study began, by only one person determining volumes for all animals, and by estimating volumes for a large number of animals.

The number of each prey type in the gut was counted whenever the state of digestion permitted. Since most of the prey consisted of individual animals, enumeration was usually possible. Colonial organisms, such as hydroids, were counted as clumps. If an opisthobranch buccal mass was found with no body attached, it was considered one animal.

The data were then separated by depth range, by season, and by size class. The depth ranges were 30–49 m, 50–69 m, and 70–100 m. The seasons were established as winter (December–February), spring (March–May), summer (June–August), and fall (September–November).

Because some of the seasons showed no statistical differences in feeding habits when compared, they were combined into one. The size classes were established at approximately 10 g intervals with the first interval set at 0.01–9.99 g. These size classes were used to compare size frequency of *P. californica* throughout the depths and seasons. The size classes used in the feeding analysis were arbitrarily established as small, 0.01–10 g, medium, 11–50 g, and large, 51–450 g.

Statistical Analysis

An individual Index of Relative Importance (IRI) for each prey type was calculated for all animals as a combination of its percent numerical importance (%N), percent volumetric importance (%V), and percent frequency of occurrence (%FO) (Pinkas et al., 1971; Ambrose, 1976; Stevens et al., 1982; Haefner, 1990). Individual IRIs were calculated for the overall diet of *P. californica,* as well as for the diet at different depths, seasons, and size classes. A total IRI value was then calculated for each depth, season, and size class by adding the individual IRI values for each prey type, and from this total a %IRI value was determined for each prey type.

The percent numerical importance (%N) of each prey type used in the IRI was the average percent number of prey in each gut. For each *P. californica* the percent volume (%V) contribution of each prey type was multiplied by the percent fullness [(%V)(%F)] of gut. The product was used in place of (%V) in the individual IRIs. Because of the large variation in size of *P. californica,* it was important to include the percent fullness of gut. Prey from a large *P. californica* could make up 100% of the volume in the gut but only fill the gut to 5% fullness, whereas that same prey in a small animal could still be 100% of the volume but fill the gut to 100% fullness.

The individual IRIs were calculated by the following formula:

$$IRI = [\%N + (\%V)(\%F)](\%FO)$$

Kruskal-Wallis tests (Zar, 1984) were used to determine significance for the (%V)(%F) values for prey types within the different depths, seasons, and size classes.

The Brillouin formula (Hurtubia, 1973; Zar, 1984) was used to measure prey trophic diversity (H) found in specimens of *P. californica.* The Brillouin based evenness measure (J) was calculated from Hurtubia (1973) and Zar (1984). The H and J values were calculated from the combined numbers of individual prey in each prey type for all specimens of *P. californica* collected from each depth, season, and size class.

RESULTS

A total of 356 specimens of *Pleurobranchaea californica* was collected and dissected. The largest of the specimens weighed 411 g and the smallest weighed 0.01 g (Figure 2). The largest number (n = 147) of animals weighed in the range of 1.1–50 g. There was also a large number of animals weighing less than 1 g (n = 137), and no animals weighing 251–300 g (Figure 2).

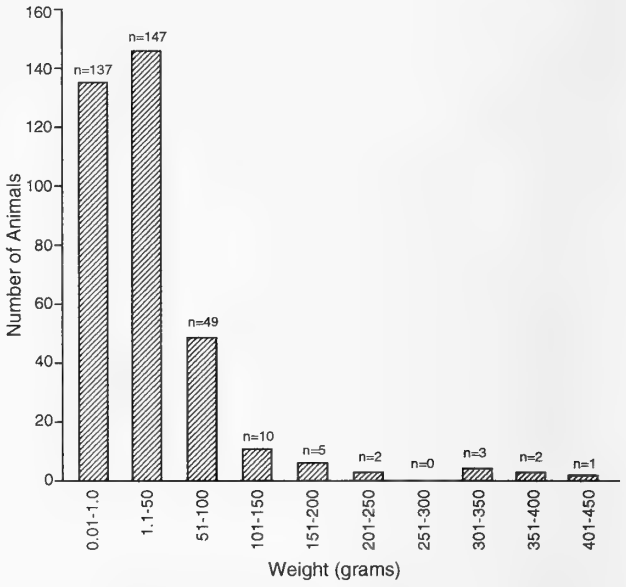

Figure 2

Size-frequency of all individuals of *P. californica* collected. *n* = the total number of individuals in each size class.

The size of animals collected varied little with depth (Figure 3). Within each season, similar size classes could be found at all depths. The size of animals collected did change with season (Figures 3, 4). In January the average size was 95.2 g (± 18.3 g, n = 35), which was the highest average size of the year. The average size remained high until May when it began to decrease (Figure 4a). By August the average size was at its lowest of the year (2.7 ± 2.3 g, n = 23). The average size began to increase again in November.

From spring to summer there was a decrease in the number of animals collected weighing above 10 g (Figure 3). During fall, specimens of *P. californica* weighing less than 10 g were collected from all depths but increased from eight animals collected at 30–49 m to 44 animals collected at 50–69 m to 94 animals collected at 70–100 m (Figure 3). The average number of animals collected per trawl tended to be low (Figure 4b) when the average size of *P. californica* was at its highest (January–May, Figure 4a). The lowest average number of animals caught per trawl was in June (0.83 ± 0.4 animals/trawl, *n* = 10). The average number of animals collected per trawl increased from July (2.7 ± 0.6 animals/trawl, *n* = 43) until October when it reached its highest point (6.9 ± 2.4 animals/trawl, *n* = 96) (Figure 4b).

Of the 356 specimens, 237 had material in their guts, and there were no signs of regurgitation from any spec-

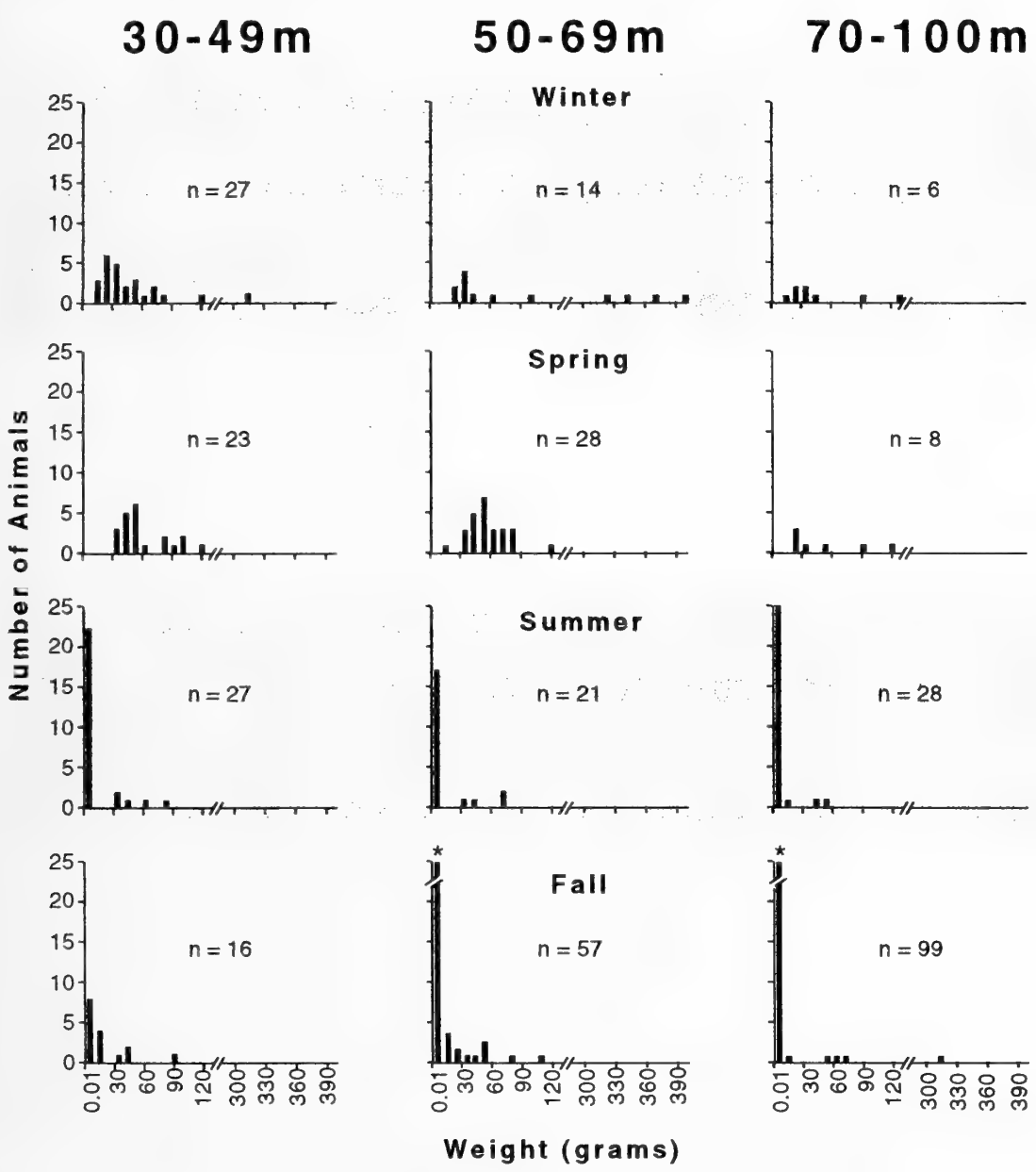

Figure 3

Size-frequency of individuals of *P. californica* collected in each season and at each depth. Size classes of 150–290 g have not been included. n = the total number of animals. * = total number of animals in 0.01–9.9 g size class for 70–100 m during the fall is 94 and for 50–69 m in the fall is 44.

imens. Of the 237, however, 100 had only sediment in their guts and were not used in the feeding analysis.

Fifty percent (± 6%, n = 62) of the animals weighing 0.01–1.0 g had empty guts. In addition, the digestive tract did not seem well developed in some of the smallest specimens, and in two cases, no digestive system was found when the animals were dissected. Empty guts occurred less frequently in the animals weighing 1.1–200 g. The presence or absence of food in the guts of the largest animals showed large variations because of the small number of animals collected in these size classes. For example, the single animal found that weighed between 401–450 g had prey in its gut, whereas the two animals found that weighed between 351–400 g (Figure 2) had nothing in their guts.

The percent of animals with stomach contents had its

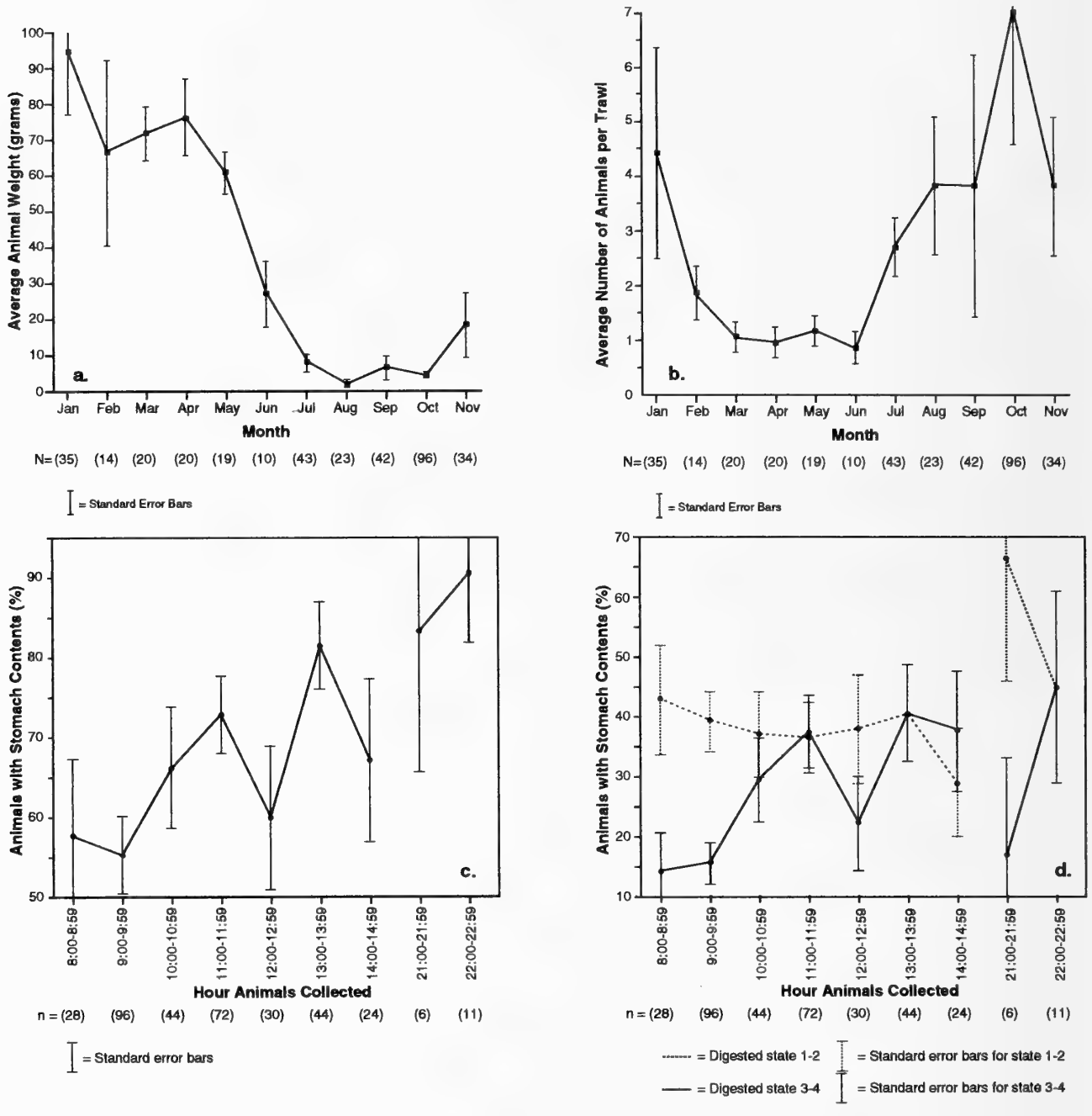

Figure 4

a. The average weight (grams) of *P. californica* individuals, per trawl, for each month the animals were collected. (#) = n, the total number of animals collected in each month. b. The average number of animals of *P. californica* per trawl, for each month the animals were collected. (#) = n, the total number of animals collected in each month. c. Percentage of *P. californica* with stomach contents for each hour of collecting. (#) = n, the total number of animals collected in each hour. n = 1 at time 00:00–00:59 (not shown). d. Percentage of *P. californica* with stomach contents in digested state 1–2 or 3–4 for each hour collected. Digested states 1–2 = well digested, some prey parts recognizable. Digested states 3–4 = little digested, whole prey recognizable. (#) = n, the total number of animals collected in each hour. n = 1 at 00:00–00:59 not shown.

highest values during the time intervals of 1100–1159 (73.6% ± 5.2%, $n = 72$) and 1300–1359 (81.8% ± 5.9%, $n = 44$) (Figure 4c). From 0900–0959, *P. californica* had the lowest percent of animals with stomach contents (55.2% ± 5.1%, $n = 96$) (Figure 4c). The time periods of 2100–2159 and 2200–2259 both had high values for percent of animals with stomach contents, but the standard errors were also high because of the small number of animals collected from these time periods.

The percent of *P. californica* with stomach contents in digestion states 1 and 2 (medium to advanced digestion) stayed fairly constant when plotted against collecting time (Figure 4d). The percent with stomach contents in digestion states 3 and 4 (no to early digestion) started off low (14.3% ± 6.8%, $n = 28$,) in the morning hours (0800–0859) and increased to its highest values between 1100 and 1400 (37.5% ± 5.8%, $n = 72$, for the time 1100–1159 and 40.9% ± 7.6%, $n = 44$, for the time 1300–1359) (Figure 4d). The percent with stomach contents in digestion states 3 and 4 declined again from 2100–2159 (Figure 4d), but these data may be suspect because there were very few animals collected at this time.

Fourteen recognizable prey types from six different phyla were found in the digestive tracts of the 137 specimens used for feeding analysis (Table 2). There were also two unrecognizable categories which we called digested material and unknowns.

The most common identifiable food items in the guts of *P. californica* were *Pleurobranchaea californica* (as prey) and *Armina californica* (Cooper, 1863) (Figure 5). These two species contributed the greatest volume and highest numerical importance and occurred most frequently. There were eight other prey types of lesser importance (Figure 5). Gastropods, copepods, and crustaceans were found in only a few specimens of *P. californica* (Table 2). Five lesser prey types, unknown opisthobranch, egg mass, sea pen, nemertean, and pleuronectid fish, were each found in one specimen of *P. californica* (Table 2).

The diet of *P. californica* varied little with depth because the two most common prey types dominated at all depths (Figure 6). *Armina californica* was found in specimens of *P. californica* from all three depth ranges, but at 50–69 m, its %IRI was highest at 60.5% (Figure 6) and its (%V) (%F) value (1341.0% ± 381.0%, $n = 60$) was significantly higher than at the other depths (Kruskal-Wallis, $P < .05$).

Aglaja sp., unknowns, and polychaetes were also found

Table 2

Taxa of the prey from *P. californica* and the number of specimens of *P. californica* found with that prey type.

Taxon	Prey	Number of *P. californica* with prey type
Mollusca		
Gastropoda	Unknown species	6
Opisthobranchia	Unknown species	1
Cephalaspidea	*Aglaja* sp.	16
Notaspidea	*Pleurobranchaea californica*	30
Nudibranchia	*Armina californica*	26
Cephalopoda	Squid egg mass	1
Annelida		
Polychaeta	Phyllodocids, Capitellids, Terebellids and Sabellids	11
Arthropoda		
Crustacea		
Malacostraca		
Peracarida	Unknown species	2
Amphipoda	Caprellids	9
Maxillopoda		
Copepoda	Unknown species	3
Cnidaria		
Hydrozoa	Unknown species	14
Anthozoa	Sea Pen, unknown species	1
Teleostei	Pleuronectid, unknown species	1
	Unknowns	18
	Digested material	41

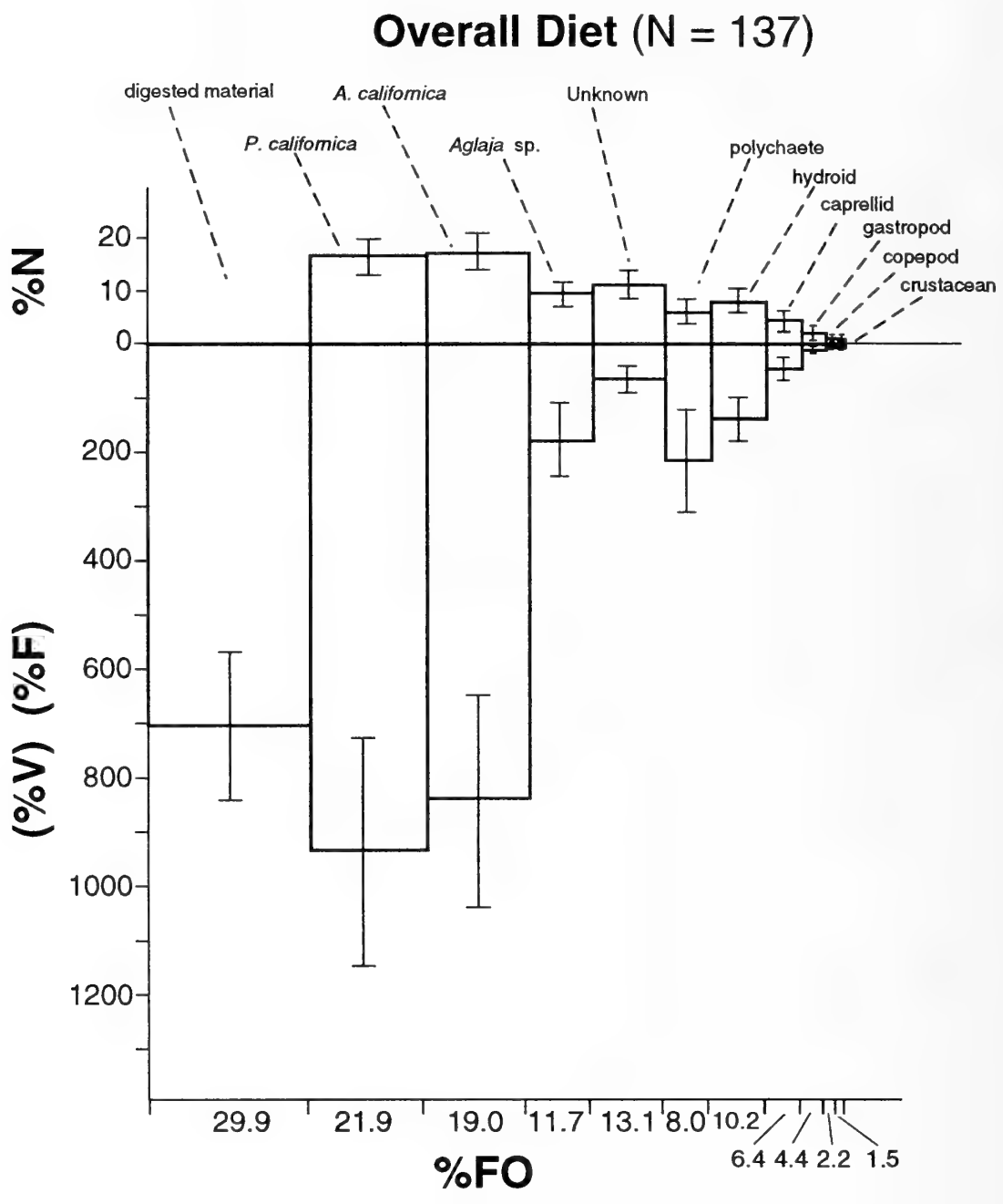

Figure 5

Individual Index of Relative Importance (IRI) for the overall diet of *P. californica*. N = the total number of animals analyzed that had stomach contents other than just sediment.

in specimens of *P. californica* from all depths. At 30–49 m and 50–69 m (Figure 6), *Aglaja* sp. made up only a small part of the diet, but at 70–100 m, *Aglaja* sp. had a larger %IRI value (11.8%) than *A. californica* (9.3%) (Figure 6).

Specimens of *P. californica* collected in winter (January–February) had very similar diets to those collected in spring (March–May); likewise, specimens of *P. californica* collected in summer (June–August) had very similar diets to those collected in fall (September–November). Differences in the diet of *P. californica* became apparent when the seasons were combined, for most prey types,

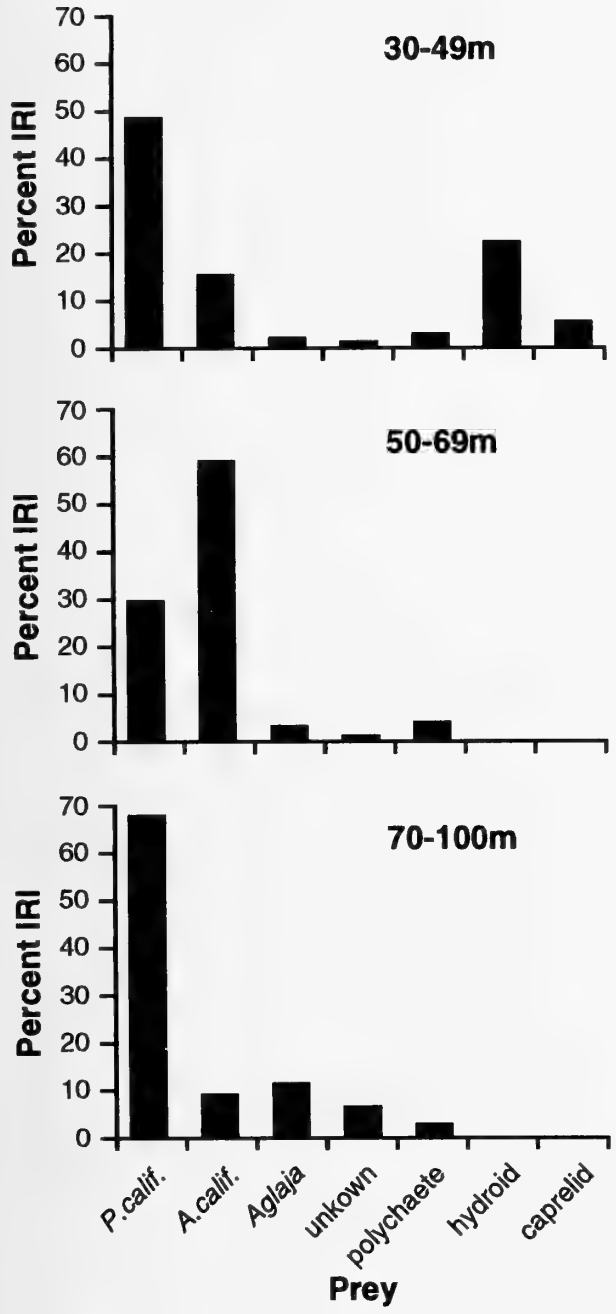

Figure 6

Percent Index of Relative Importance for identified prey found in specimens of *P. californica* collected at the three different depth ranges.

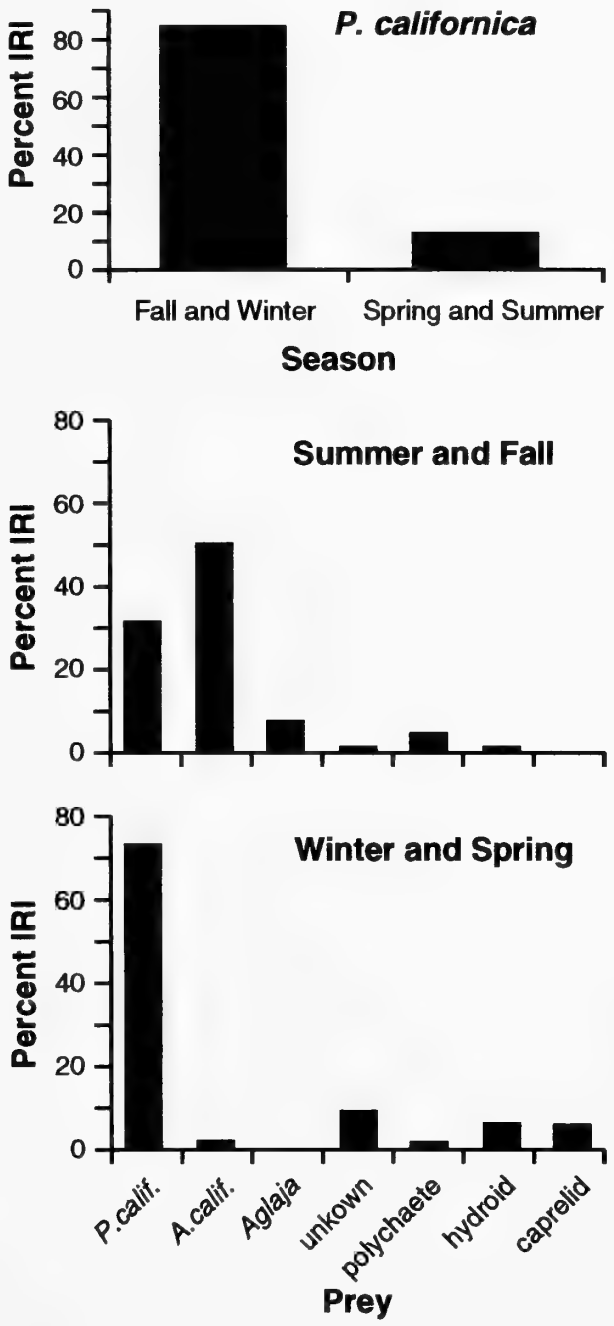

Figure 7

Percent Index of Relative Importance for identified prey items found in specimens of *P. californica* collected in fall and winter and spring and summer for *P. californica* as prey and for the summer and fall and winter and spring for all prey items.

into winter-spring and summer-fall, and for *P. californica* (as prey), into fall-winter and spring-summer (Figure 7).

Armina californica was eaten by specimens of *P. californica* in all seasons, but the (%V)(%F) value (1281.6% ± 299.1%, n = 87) from summer-fall was significantly higher than the value from winter-spring (80.0% ± 46.0%, n = 50) (Kruskal-Wallis, $P < .05$). *Armina. californica* also had a higher %IRI value in summer-fall (51.6%) than in winter-spring (2.6%) (Figure 7).

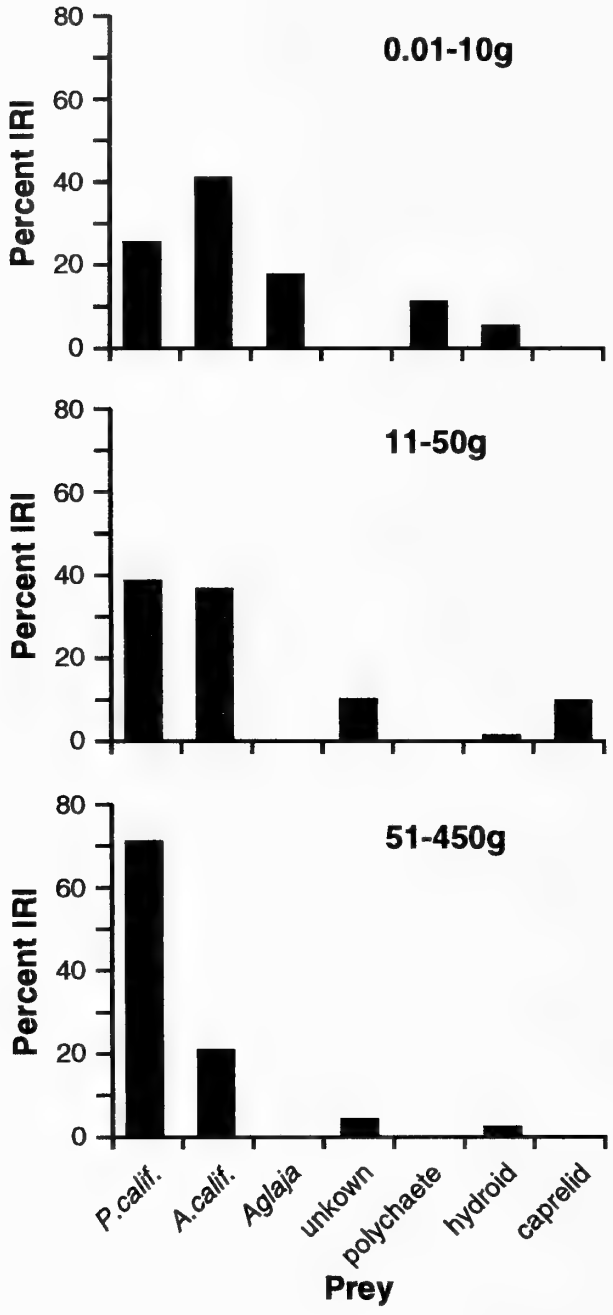

Figure 8

Percent Index of Relative Importance for prey found in specimens of *P. californica* in the three different size classes.

Aglaja sp. had a 17.2% frequency of occurrence in summer-fall but was only found in one *P. californica* in winter-spring (Figure 7).

Pleurobranchaea californica ate many of their own species throughout the year. The %IRI values for *P. californica* (as prey) did show a difference between winter-spring (73.9%) and summer-fall (32.7%) (Figure 7), but the difference was magnified when the values for fall-winter (86.7%) were compared with spring-summer (13.3%) (Figure 7).

Table 3

Pleurobranchaea californica trophic diversity and evenness summary by depth, season, and size class. n = total number of individual prey items. k = total number of prey categories. H = Brillouin measure of diversity. J = Brillouin based evenness measure.

Depth/season/ size class	n	k	H	J
70–100 m	49	9	0.684	0.766
50–69 m	92	10	0.704	0.751
30–49 m	144	13	0.638	0.608
Winter	47	7	0.478	0.579
Spring	56	11	0.692	0.746
Summer	86	10	0.684	0.702
Fall	94	12	0.752	0.703
51–450 g	99	10	0.703	0.855
11–50 g	63	8	0.632	0.700
0.01–49 g	121	9	0.692	0.746

The diet of *P. californica* was also affected by the size of the animal (Figure 8). The diet of *P. californica* weighing 51–450 gm was the most specialized and was dominated by individuals of its own species (Figure 8) as can be seen by a significantly higher %IRI value for *P. californica* (as prey) from the 51–450 g size class compared to the other size classes (Kruskal-Wallis, $P < .05$).

Armina californica was eaten by specimens of *P. californica* from all size classes but in significantly greater numbers in the smallest size class. *Aglaja* sp. was not eaten by any specimens of *P. californica* over 51 g and was consumed by only one animal between 11 and 50 g. *Aglaja* sp. was only important in the diets of animals from the smallest size class (Figure 8). Polychaetes were consumed by only one animal from each of the size classes: 51–450 g and 11–50 g. However, small polychaetes were important in the diet of the smallest *P. californica* (Figure 8).

Diet diversity indicated that the specimens of *P. californica* from 50–69 m had the most diverse diets, whereas the specimens of *P. californica* from 30–49 m had the lowest diet diversity (Table 3). The evenness value, J = 0.766, was highest at 70–100 m and decreased to 0.751 (50–69 m) and 0.608 (30–49 m) (Table 3).

The trophic diversity for specimens of *P. californica* from different seasons was at its lowest, 0.478, in winter (January–February) and increased to 0.752 in fall (September–November) (Table 3). The highest evenness value, 0.746, was in spring (March–May) and the lowest value, 0.579, in winter (January–February) (Table 3). Specimens of *P. californica* from the 11–50 g size class

had the lowest trophic diversity value, 0.632, and the lowest evenness value, 0.700 (Table 3). The largest size class, 51–450 g, had the highest diversity value, 0.703, and the highest evenness value, 0.855 (Table 3).

DISCUSSION

Opisthobranchs make up the largest portion of the identifiable diet of *P. californica.* By contrast, Willan (1984) in a review of the food habits of the order Notaspidea, reported that other species of *Pleurobranchaea* favored cnidarians, and Cattaneo-Vietti et al. (1993) reported that individuals of *Pleurobranchaea meckelii* Leue, 1813, in the Mediterranean Sea favored cnidarians over other prey types. Willan (1984) suggested that members of the genus are opportunistic. We found that although *P. californica* does ingest cnidarians, it seems to prey more often on opisthobranchs than on other food sources (Figure 5).

Of interest is the finding that *P. californica* is cannibalistic. *P. californica* has been reported to be cannibalistic in the laboratory (Coan, 1964; Chivers, 1967), but this is the first evidence that *P. californica* is also cannibalistic in nature. Twenty-two percent of the specimens consumed individuals of their own species (Figure 5).

Cannibalism seems to be natural and seems unlikely to have occurred in the net during collection. The specimens of *P. californica* consumed as prey were usually found whole but digested enough that they could be recognized only by their buccal mass and radula. Digestion in *P. californica* is apparently very slow. Morse (1984) found that an animal consumed by *P. californica* could still be found in the gut after 14 days. When the slow digestion rate of *P. californica* is compared with the digestion that had occurred on specimens of *P. californica* (as prey) and the time the nets were in the water, less than 30 min, it is very unlikely that cannibalism had occurred in the net.

Cannibalism is usually considered a destructive force in a population because animals can potentially eat their own progeny or mates, but there are benefits, which in some species outweigh the costs (Fox, 1975a). Cannibalism can act as a mechanism for population control that decreases the numbers of intraspecific competitors almost immediately when food becomes scarce (Fox, 1975b). Tsubokawa & Okutani (1991) reported that *Pleurobranchaea japonica* Thiele, 1925 juveniles are cannibalistic, and individuals displaying this tendency grow much larger than others. A larger animal would have a better chance in competition for food. Paine (1965) reported that in *Navanax inermis* (Cooper, 1862) when cannibalism is confined to predation by larger individuals on only young life history stages, it permits the reproductive stages to live in an environment in which their local food supply is not apt to be seriously limited through competition with conspecifics.

Cannibalism has been considered a laboratory artifact and not common in nature (Dionne, 1985; Meffe & Crump, 1987). Fox (1975a), however, reported that cannibalism was not an aberrant behavior but a normal response to environmental factors. Cannibalism is now considered common and widespread. It has been found in 1300 species (Jones, 1982), ranging from protozoa to mammals (Polis 1981). Fox (1975a) found that there were many mentions of occasional cannibalism acts by marine animals, but detailed feeding records were available for relatively few.

Cannibalism by specimens of *P. californica* seemed to be more common in fall and winter (September–February, Figure 7), probably because there were more small *P. californica* (as prey) available to eat in those months (Figure 4a, b). Trawl data suggest that the number of *P. californica* available for consumption began increasing in summer (Figures 3, 4b). This increase of animals could possibly be due to juveniles settling from the plankton similar to *Pleurobranchaea japonica,* which has planktonic larvae that settle to the bottom as juveniles (Tsubokawa & Okutani, 1991). In spring and summer (March–June) the number of available *P. californica* (as prey) decreased (Figure 4b), which could suggest that post-spawning mortality had occurred.

Although specimens of *P. californica* (as prey) were eaten by all size classes (Figure 8), of *P. californica,* the animals weighing over 100 g, seemed to consume them to the exclusion of most other prey. Polis (1981) reported that, in general, larger animals are more voracious cannibals than smaller animals. Individuals of *P. californica* (as prey) might be favored by the largest specimens of *P. californica* because, compared to the other prey types, specimens of *P. californica* (as prey) were more abundant and usually larger, thus making a larger meal. Paine (1965) reported that cannibalism by *Navanax* was associated with size differences, and that *Navanax* could live on cannibalism alone. Paine (1965) also found that large *Navanax* gradually lose their ability to physically manipulate and swallow small prey. The largest specimens of *P. californica* might also have this problem, causing them to favor the larger *P. californica* (as prey) over other smaller prey.

Armina californica was the second most frequently eaten prey type of *P. californica. Armina californica* has been found to burrow under its own prey (Bertsch, 1968) and to burrow in the sand (Ricketts et al., 1985). Because *P. californica* swallows its prey whole, sediment, along with the main prey in the case of sand-dwelling or buried *A. californica,* will be ingested. Sediment was found in the stomachs of most of the specimens of *P. californica* dissected. The sediment was thoroughly examined, but no evidence of spicules, setae, or other identifiable parts could be found. Sediment in the stomach of specimens of *P. californica* would seem to be a result of *P. californica* ingesting or attempting to ingest prey items that live on or below the substratum.

Specimens of *A. californica* were eaten by specimens

of *P. californica* from all depths but most often by specimens of *P. californica* from 50–69 m (Figure 6). The diet of *A. californica* consists of sea pansies, *Renilla kollikeri* (Bertsch, 1968; Eyster, 1981; Ricketts et al., 1985), and sea pens (Birkeland, 1974; Ricketts et al., 1985). While *R. kollikeri* does not occur in Monterey Bay, the sea pens *Acanthoptilum gracile,* ranging to depths of 91 m, and *Stylatula elongata,* ranging to depths of 65 m, can be found in Monterey Bay (Ricketts et al., 1985). Since the largest numbers of sea pens were caught in our trawls between 50–69 meters, *A. californica* might be expected to be most abundant in that depth range and therefore more available to *P. californica.*

Pleurobranchaea californica also consumed *A. californica* more often in summer and fall than in winter and spring (Figure 7). Little is known about the life histories of arminacean nudibranchs, although they probably have an annual or subannual life cycle (Eyster, 1981; Todd, 1983). The number of *A. californica* caught in our trawls increased a few months before the number of *P. californica* increased, and in those same months the number of *A. californica* being consumed by specimens of *P. californica* also increased (Figure 7). If *A. californica* has an annual life cycle, this increase in *A. californica* could come from the recruitment of juveniles.

Specimens of *Aglaja* sp. were eaten by specimens of *P. californica* from all depths, and, except for one individual, all were eaten in summer and fall (Figure 7). The increase in number of *Aglaja* sp. consumed in summer and fall could correlate with recruitment, similar to that of *A. californica,* or to the fact that there were more small individuals of *P. californica* as predators. Specimens of *Aglaja* sp. were eaten mostly by the smallest *P. californica* (Figure 8). Specimens of *Aglaja* sp. were abundant in the trawls but they were never larger than approximately 1 cm in length (personal observation). If Paine (1965) is correct, the small size of these animals could make it difficult for the large specimens of *P. californica* to manipulate and swallow them.

Polychaetes are abundant in sedimentary environments throughout the world (Fauchald & Jumars, 1979). Polychaete remains appeared in the guts of specimens of *P. californica* at all depths and throughout the year, but most were eaten by only the largest members of the smallest size class, 0.01–10 g (Figure 8). Most adult polychaetes appeared to be too large for the smallest individuals of *P. californica* to eat whole. In contrast the largest specimens of *P. californica* might have been unable to manipulate and swallow the polychaetes (Paine, 1965), or they possibly bypassed the polychaetes to search for larger, more accessible prey. The polychaetes found in the guts of specimens of *P. californica* were also too large for small opisthobranchs like *Aglaja* sp. to eat. This makes it unlikely that the polychaetes found in individuals of *P. californica* came from the digestive tracts of other opisthobranchs which had been consumed and digested by specimens of *P. californica.*

Hydroids and caprellids were both found in the guts of specimens of *P. californica.* Because Willan (1984) and Cattaneo-Vietti et al. (1993) reported that specimens of *Pleurobranchaea* favor cnidarians, it is possible that individuals of *P. californica* were preferentially consuming the hydroids and incidentally consumed the caprellids with them. Since this study indicates that specimens of *P. californica* seem to favor opisthobranchs, and since eolid nudibranchs characteristically prey on cnidarians (Ricketts et al., 1985), it is also possible that specimens of *P. californica* were trying to catch other nudibranchs and inadvertently ingested the hydroids and caprellids instead.

Scavenging has also been suggested by Willan (1984) as a possible feeding technique for *Pleurobranchaea* species. Cattaneo-Vietti et al. (1993) found that the presence of highly motile organisms, such as fish and squid, in the diet of *Pleurobranchaea meckelii* strongly suggested that *P. meckelii* is a scavenger. Cattaneo-Vietti et al. (1993) also suggested that in areas of commercial trawling, such as Monterey Bay, the scavenging behavior could be magnified. The fish and squid egg mass found in the guts of *P. californica* suggest that *P. californica* is also a scavenger.

In nature, *P. californica* seems to feed during both day and night. A high percentage of specimens of *P. californica* collected in daylight hours had food in their guts (Figure 4c), and although we obtained only a small amount of data for night time periods, they suggest that a high percentage of specimens of *P. californica* collected during late night hours also had food in their guts (Figure 4c). Since digestion in *P. californica* can take up to 14 days (Morse, 1984), the presence in the gut of multiple food items, in obviously different states of digestion, suggests that specimens of *P. californica* keep eating even if they still have not digested the food already consumed.

The population of *P. californica* from depths of 50–69 m had the highest diet diversity (Table 3) and consumed more prey items than those from 70–100 m. Although the population of *P. californica* from depths of 30–49 m had consumed more prey items than those from 50–69 m (Table 3), the diversity was lower because most of the prey items came from one prey type. *P. californica* had its highest diet diversity in fall (Table 3) unlike *Pleurobranchaea meckelii* which has its lowest diet diversity in summer and fall (Cattaneo-Vietti et al., 1993). The diet diversity of *P. californica* was high in fall because the specimens of *P. californica* taken at that time had consumed at least one of almost all the different prey types (Table 2). The largest size class of *P. californica* had highest diet diversity and the most even diet reflecting the many prey types which were eaten in equal quantities. By contrast, individuals of *P. californica* from the 11–50 g size class consumed fewer prey items and fewer prey types.

The large increase of tiny specimens (0.01 g) of *P. californica* caught beginning in July (Figure 4a, b), when they were large enough to be caught in the net, suggests that recruitment happens in early summer at all three depth ranges (Figure 3). The number of tiny specimens of *P. californica* collected in fall increased at deeper depths (Figure 3). The increase in the number of animals collected at deeper depths was probably influenced by an increase in the number of trawls done at deeper depths and by the animals having a patchy distribution (personal observation). A patchy distribution is suspected because some trawls collected many tiny specimens of *P. californica* while other trawls collected no specimens of *P. californica.*

Tsubokawa & Okutani (1991) found that adult specimens of *P. japonica* died after laying eggs. If postspawning mortality also occurs in *P. californica,* then the months in which egg masses would be found should correspond to a decrease in the number of animals caught. *Pleurobranchaea californica* had a decrease in the number of animals caught between February and June (Figure 4b), which would suggest post-spawning mortality. Although the data suggest that *P. californica* has postspawning mortality, it does not appear to be total. In July through October, some large specimens of *P. californica* were still being caught in the nets when mostly small specimens were being collected. This suggests that *P. californica* may have generation overlap. Cattaneo-Vietti et al. (1993) found generation overlap in *Pleurobranchaea meckelii* and suggested that *P. meckelii* has a biennial life cycle. The generation overlap in *P. californica* suggests that *P. californica* may also have a biennial life cycle.

CONCLUSIONS

The data suggest that specimens of *Pleurobranchaea californica* are cannibalistic and euryphagic in Monterey Bay consuming a variety of organisms. The gut contents of *P. californica* collected contained 16 different taxa of which three opisthobranchs were the most abundant. The three opisthobranchs consumed were *P. californica* (as prey), *Armina californica,* and *Aglaja* sp. Sediment occurred in a large number of animals but appeared to be a result of *P. californica* eating prey items that live on or below the substratum. Specimens of *P. californica* were found to take similar prey at all depths. The diet of *P. californica* was not found to change with seasons, and the different size classes of *P. californica* were found to eat different prey. The data also suggest that *P. californica* may be a scavenger and have a biennial life cycle.

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William Healey Dall: A Neo-Lamarckian View of Molluscan Evolution

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Abstract. Throughout his career William H. Dall attempted to reflect evolutionary relationships in his molluscan classifications. From 1865 to 1877 Dall's evolutionary scenarios were built almost exclusively around heterochronic processes (primarily peramorphosis). Biogeographic congruence and natural selection were also invoked. The patterns Dall saw and the processes he inferred were probably derived from the training he received from L. Agassiz and others at the Museum of Comparative Zoology, Harvard University. By 1882 Dall had formalized his heterochronic arguments in terms of Edward Cope and Alpheus Hyatt's patterns of acceleration and retardation. Variation and *de novo* structures appeared through the interaction of physical forces with the organism, and were passed on to progeny by the inheritance of acquired characters. By 1882 Dall was an active participant in the Neo-Lamarckian movement in America. Dall's evolutionary models determined how he evaluated character state polarities, transformations, and their import. In his monographs and revisions he ordered his species and higher taxa from "primitive" to "derived," reflecting his best interpretation of their "natural order." The recognition of Dall's intent and the rules by which he interpreted history require us to carefully consider the implications of using his classifications today in evolutionary studies.

INTRODUCTION

William Healey Dall (1845–1927) was one of the great, late nineteenth- and early twentieth-century American naturalists. Like many naturalists of his time, his expertise spanned a broad array of taxa, geologic epochs, and biological thought. His contributions are to a variety of fields, including physical and cultural anthropology, oceanography, paleontology, and invertebrate and vertebrate zoology. He published over 1600 papers, reviews, and commentaries in many of the most prestigious journals of his day, such as *Nature, Science, American Naturalist, Proceedings of the National Academy of Sciences,* and various publication series of the Smithsonian Institution (Bartsch et al., 1946). His expedition and fieldwork centered in Alaska, but he also conducted field studies in Nicaragua and along both the east and west coasts of the United States. He was an elected member of numerous American societies, including the American Association for the Advancement of Science, National Academy of Sciences, National Geographic Society, Philosophical Society of Washington, as well as numerous European societies whose meetings he attended during his travels abroad.

Although Dall was an expert in many areas of natural history, his greatest scientific contributions were in the field of malacology. As a malacologist working on both fossil (Tertiary) and living mollusks, W. H. Dall described over 5300 species (Boss et al., 1968). Many of his publications were short taxonomic papers, but several were comprehensive monographs, including anatomical descriptions and phylogenies of the taxa under consideration. Unlike most other pioneer American malacologists, Dall was interested in the evolutionary relationships of the taxa with which he worked. In two papers on the phylogeny of Docoglossa (i.e., Patellogastropoda of Lindberg, 1988a) published in 1871 and 1876 we get a glimpse of his evolutionary thinking. Like many biologists of his day, Dall accepted evolution but thought Darwin's theory did not fully explain its causes.

My purpose is to examine Dall's evolutionary thinking as demonstrated in his published papers, addresses, reviews, and personal correspondence. My interest was stimulated by the fact that we both have worked on the same group of gastropods—namely the Patellogastropoda (Dall's Docoglossa). However, our respective hypotheses of relationships are diametrically opposed (Figure 1), and although both of our approaches are evolutionary in intent and argument, the discrepancy in our respective results begs explanation. Moreover, insights into Dall's evolutionary philosophy may help us evaluate his other systematic work and taxonomic groupings, many of which remain in use today.

W. H. DALL THE EVOLUTIONIST

William H. Dall published five papers that dealt primarily with evolution. Two of these papers (1877a, 1890) were essentially theoretical, while the remaining three (1882, 1889, 1894) featured molluscan exemplars in the discussion of evolutionary mechanisms.

In Dall's (1877a) first evolution paper he moved closer

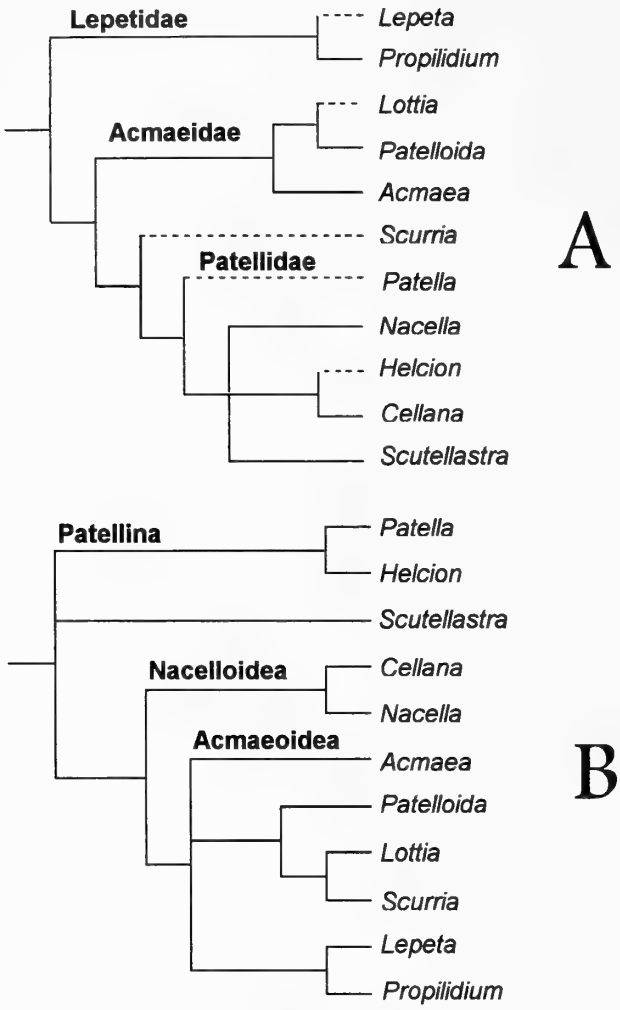

Figure 1

Phylogenetic relationships among the Patellogastropoda. A. Dall's (1876 Figure 2) genealogical tree redrawn as a cladogram; stippled branches have 0 length. B. Cladogram based on parsimony analysis of the Patellogastropoda (redrawn from Lindberg & Hedegaard [1996]). See Table 1 for synonyms and equivalent taxon names.

to fully embracing Darwin's theory of natural selection than he did in his earlier taxonomic papers mentioned above. He began by proposing a hypothesis to account for "missing links in the chain of development," a pattern that he regarded as the "chief weapon of all opponents" of natural selection (Dall, 1877a:135). This defense of a theory that he had regarded as "plausible but highly unsatisfactory . . ." only 6 years earlier marks Dall's closest encounter with pure Darwinian evolution. Dall, aware of the absence of intermediate types in the fossil record, had been seeking a mechanism that would produce "leaps, gaps, saltations . . . for some years . . ." He termed his new mode of evolution "saltatory evolution."

Table 1

Synonyms and equivalents of Dall's (1871) taxa (Figure 2) used for cladogram construction in Figure 1.

Figure 1. Lindberg (1988a, 1998)	Figure 2. Dall (1871)
Lepeta, in part	*Cryptobranchia* Middendorff, 1851
Propilidium Forbes, 1859	*Pilidium* Forbes, 1859
Lepeta, in part	*Lepeta* Gray, 1847
Lottia, in part	*Collisella* Dall, 1871
Patelloida Quoy & Gaimard, 1834	*Collisellina* Dall, 1871
Acmaea	*Acmaea* Eschscholtz, 1833
Lottia, in part	*Lottia* Gray, 1833
Scurria	*Scurria* Gray, 1847
Patella	*Patella* Linné, 1759
Nacella, in part	*Nacella* Schumacher, 1817
Nacella, in part	*Patinella* Dall, 1871
Helcion, in part	*Patina* Leach, 1852
Helcion, in part	*Helcion* Monfort, 1810
Cellana H. Adams, 1889	*Helcioniscus* Dall, 1871
Scutellastra H. & A. Adams, 1854	*Ancistromesus* Dall, 1871

Dall began with a paradox outlined by Edward Cope (1868) in his paper "On the Origin of Genera." Cope had distinguished two distinct evolutionary engines. The laws of acceleration and retardation (see Gould, 1977:85) guided the origin of genera, while the origin of species was determined by natural selection. These engines operated independently of one another. Thus, in Cope's view it was possible "that at times *the change of generic type has taken place more rapidly than that of specific, and that one and the same species . . . has, in the natural succession, existed in more than one genus*" (Cope, 1868:272). This rapid change or leap would leave no intermediate forms and this is what Dall sought to explain. Dall concluded that saltations were "perfectly in accordance with the view that all change is by minute differences gradually accumulated in response to the environment . . ." (Dall, 1877a:136). This is in marked contrast to Cope's assertion that the mechanisms that would produce such leaps (acceleration and retardation) were independent of natural selection. In today's idiom, Dall sought a model to explain a macroevolutionary pattern that did not negate microevolutionary processes.

Dall's paper also contained some other seemingly modern components. For example, Dall recognized aspects of stasis in the fossil record and the rapidity in which character change would take place, aspects of evolution that would much later fall under the rubric of punctuated equilibrium (Eldredge & Gould, 1972). He also began his hypothesis with a clearly stated species concept, ". . . similar individual organisms in which for the time being the majority of characters are in a condition of more or

less stable equilibrium; and which have the power to transmit these characters to their progeny with a tendency to maintain this equilibrium" (Dall, 1877a:136).

Dall's hypothesis required that this tendency to maintain equilibrium be strong enough to resist gradual changes in the environment until a point where a critical threshold was achieved and there was then a massive reorganization within the animal followed again by stasis. Dall likened this phenomenon to the damming of water behind debris in a gutter that ultimately would break through the dam only to reform and repeat the event behind additional debris farther downstream. However, the dam was never completely watertight, and small continuous trickles existed between these events.

This variation and differential transmission of the tendency to maintain character states would produce a divergence within a species, one population (the trickle) accumulating character state changes gradually as it tracked the environment while the other (behind the dam) remained relatively unchanged until a rapid, punctuated event. The populations that tracked the environmental changes on the microevolutionary level would be better adapted and "able to persist" through the breaking of the dam. Those populations in stasis until the dam break undoubtedly had a "broader base," i.e., less specialized, and were "less injuriously affected by *adverse* circumstances and consequently might still endure" across the event as well. Intermediate individuals would be the "least fitted to persist" and would be "rapidly eliminated." Through this model Dall envisioned "a parallel series of species in two or more genera, existing simultaneously." Dall closed his paper with a call for the study of stasis ("inherited tendency to equilibrium") pointing out that the "inherited tendency to vary" was receiving all the attention.

It is likely that Dall first noted examples of Cope's paradox while working on brachiopods rather than mollusks. Dall (1877b) discussed brachiopod species pairs that had identical specific characters, but belonged to two genera—*Terebratella* d'Orbigny, 1847, and *Magasella* Dall, 1871. Dall noted that the similarity between these species pairs was "usually only remarkable when the *young* of the latter (*Terebratella*) is compared with the *adult Magasella*" (Dall, 1877b:164). After discussing the taxa and their distributions, Dall stated that three criteria must be met to confirm that "the relations of the one to the other in development should be in harmony with the development of the group as a whole in geological time and organic differentiation."

1. The distribution of any two species so related to each other should absolutely coincide.
2. The young should all be *Magasellae*; the adults (barring dwarfs), all the "companion genus."
3. Actual study of the embryology and young stages should be able to trace the edentulous stage into the *Magasellae* stage, and that into the final "companion" stage.

Dall presented observations falsifying all three criteria and thought that "another hypothesis will explain them, if not equally well, yet in greater harmony with the analogy of the case, and . . . with greater probability of accuracy" (Dall, 1877b:169). Dall concluded that this subject would provide the key to some important generalizations. And although he thought he had identified transformations through three genera "in the life of one individual," Dall discounted Cope and Hyatt's progressive evolution as the mechanism.

Dall's first excursion into evolutionary thought generated an unfavorable response from his friend and colleague Alpheus Hyatt at the Boston Society of Natural History. Hyatt and Dall had undoubtedly met when both were students of Louis Agassiz at the Museum of Comparative Zoology at Harvard University in 1862 (see below). Hyatt (1877a) thought Dall's paper on saltatory evolution to "misquote Cope and entirely skipped your humble servant who's specialty happens to be and has been for 16 years just the point you allude to." Hyatt went on to accuse Dall of not reading his (Hyatt's) "little pamphlets, which I so trustingly send you from time to time . . ." and of not acknowledging Herbert Spencer. Hyatt closed his letter with pleasantries, but still maintained that Dall had overstated his contribution.

It is difficult to understand Hyatt's criticism of Dall's hypothesis. Dall did not follow Cope's reasoning for the origin of genera and species, and his reference to Cope's paper is limited to proposing an alternative hypothesis to explain Cope's one species, two genera paradox. Moreover, Dall does not mention any acceleration or retardation mechanism, and to the contrary, argues that natural selection alone is sufficient to produce the paradox. Because Hyatt's "little pamphlets" also primarily dealt with Hyatt's insights into the role of acceleration and retardation in evolution, it is likewise hard to understand how Hyatt's work related to Dall's hypothesis. Whatever the source of Hyatt's irritation with Dall's saltatory evolution it apparently was soon smoothed over by a letter from Dall to Hyatt, because in less than 9 days' time Hyatt had written Dall a second letter apologizing for his hasty conclusions and promising to reread Dall's paper with greater deliberation (Hyatt, 1877b).

Five years later, in his vice presidential address to the section of biology of the American Association for the Advancement of Science meeting in Montreal, Quebec, Dall (1882) used the opportunity to state his view of evolution and the role of natural selection. Dall began by focusing on the state of malacology in America. He paid homage to Cuvier and the "immortal Lamarck" who reformed the Linnean classification and "created a science of Malacology" (Dall, 1882:4). He also recalled the resistance that he and other workers experienced when they

first began to propose classifications that reflected phylogeny: "The early students, seeking to know the relations of the animals which were huddled in a few heterogeneous genera by Linné, were the subject of no little opprobrium from the conchologists of that day, and were very generally looked upon as dangerous radicals and unsafe guides."[1] Dall continued with a summary of the state-of-our-knowledge of North American molluscan faunas by habitat, and a review of potential research programs in the field. Highlighted study areas included biogeography, the deep-sea faunas, and molluscan development and behavior (all still worthy topics today). The last study area that Dall addressed was "the subject, of which the methods applied to other forms of animal life have occupied a very large portion of the thought and activity of the scientific world for more than twenty years." Dall was speaking of "modification of organic life" and in a curious way acknowledged Darwin without ever mentioning him by name. He did this by acknowledging that the results of those studies "have revolutionized science and justly immortalized the remarkable naturalist who led the way" (Dall, 1882:10).

In contrast to his earlier paper (1877a), and unlike his treatment of Darwin, Dall acknowledged the American Neo-Lamarckian leaders by name and clearly aligned himself with them: "The labors of Cope, Hyatt, Ryder, Morse and others among us, are no less fruitful than suggestive in these directions" (Dall, 1882:11). Dall echoed Cope's and Hyatt's arguments that the characteristics on which natural selection worked were produced by dynamical evolution and "the *rhythm* of development as shown by periodic acceleration and retardation . . . ." (Dall, 1882:11). Dall even venerated Herbert Spencer. Dall's praise exactly corresponds to Hyatt's criticism of Dall's earlier paper and its lack of acknowledgments.

After these acknowledgements, Dall returned to his earlier theme of uniformity of character states between taxa and expanded it to ask the question why there were so few basic body plans, given the profusion of variation in the natural world. For Dall (1877b:12), the answer to this "mystery lies in the direct physical action of the environment, by ways and methods few of which are yet understood . . ."

Dall returned to the molluscan message of his address and revisited a topic first broached in 1871 where he noted that natural selection apparently was important in the evolution of plants, insects, and birds, but had no appreciable effect in the evolution of the Mollusca. Whereas Cope had created a dichotomy where natural selection was relegated to acting only at the species level, while the laws of acceleration and retardation worked at higher levels, Dall suggested a different dichotomy based on mental and physical prowess.

Dall considered the actions of natural, and especially sexual selection, to be far more pronounced and their effects far more important among organisms of "high mental and physical rank" interacting with each other or on "lower" organisms with which "higher forms" interact. As one example of this latter case he suggested bees and wasps interacting with plants. Dall thought simple organisms were much less subject to the actions of natural selection: "It is only when advanced to a comparatively high stage of differentiation that organisms can offer, as it were, a handle for natural selection to take hold of." (1877b: 11).

Dall viewed mollusks as an intermediate group between higher organisms (where natural selection is active) and lower animals (where it is inefficient) and therefore concluded that mollusks would make excellent exemplars for evolutionary studies.

Within the mollusks, natural selection was strongest in terrestrial snails because they interacted with higher organisms (smarter enemies) such as birds and mammals. Color patterns could be strongly selected by sighted predators. In contrast, the struggle in the sea was less violent than on land owing to the more uniform conditions of the sea, the more abundant food sources, and the less intelligent predators (mainly fishes and other mollusks). Because natural selection was not as strong here, marine species showed more variation in form, external sculpture, and coloration than terrestrial species. Protoconch sculpture and the bright colors of tropical pulmonates were under the control of some unknown evolutionary force.

However, even in marine species, natural selection could still operate, albeit in a secondary role to physical causes. Dall noted that Alaskan littorine snails exposed to heavy surf were modified with low spires, enlarged apertures, and reduced shell sculpture. Dall concluded that individuals not so modified would be removed by wave action, and thought this example "one of the most obvious instances I have observed of the action of selection among marine mollusca" (Dall, 1877:14). Dall concluded his address with a discussion of carrier shells (Xenophoridae) that have the habit of cementing bottom debris to their shells. He considered their behavior to represent an unexplainable acquisition of a valuable habit that was perpetuated by natural selection in some species, while in others it continued to persist although it was no longer useful.

This address clearly aligned William H. Dall with the Neo-Lamarckians. His earlier attempt (Dall, 1877a) to attribute both large- and small-scale morphological change to natural selection was abandoned, and the Neo-Lamarckian duet of dynamic evolution and acceleration and retardation was prominent in his world view. Although the perplexing pattern of morphological uniformity, first

[1] It is noteworthy that similar distrust of phylogenetic classifications and the workers who advocate and produce them still exists in the field of malacology today.

noted in 1877, still concerned him, another earlier theme—different evolutionary processes for "lower" and "higher" animals—resurfaced here as well. Because of Dall's international reputation in the malacological community, the influence of his evolutionary ideas was not limited to America, and a translated extract of his address appeared within 2 months in Germany (Anonymous, 1882).

In his last principal paper on evolution Dall (1890) laid out his view of dynamical evolution and argued its primary role in evolution. Dall returned to the argument that natural selection does not produce variation and contended that the physical forces and mechanical stresses placed on the organism by the environment are the sources of variation, and that these acquired characters are then inherited. Because no two individuals are ever exposed to identical environmental conditions, variation is an inescapable outcome. Dall also revisited his correlation between intelligence and the strength of the role of selection, with natural, and especially sexual, selection being more important and often more rapid in those organisms with higher "mental qualities." As before, he pointed out that only one of any pair of interacting organisms need "possess intelligence of a certain grade," but his terrestrial-snail-being-eaten-by-birds-and-mammals example was replaced by an insect/orchid example.

Dall next considered Weismann's (1882) attack on the evidence in support of the inheritance of acquired characters. Dall attempted to negate one of Weismann's points by arguing against the inheritance of mutilations and pathological characters. He chose as his example bivalve mollusks that settled in the empty burrows of rock boring taxa such as *Lithophagus* [=*Lithophaga*] and pholads. He pointed out that although they grew to conform to the "antecedent borer," he predicted that their progeny "would probably exhibit no traces of their parents' deformity." This position was contrary to Hyatt's view of the potential of pathological characters to be inherited and form a "degradational series of individuals, species and genera" (see Jackson, 1890a:926). Dall then discussed his earlier paper on the development of the bivalve hinge structure (Dall, 1889) and a forthcoming paper on the development of the columellar folds of gastropods (Dall, 1894), both of which he considered excellent examples of the dynamic influences of the environments of organisms (see below).

In a note added after his paper was read before the Biological Society of Washington, Dall reported that the Darwinians Lankester and Weismann (both strong critics of dynamical evolution) had recently suffered serious setbacks in their championing of natural selection over Neo-Lamarckism. Dall's satisfaction with this state of affairs is expressed in his addendum:

> In fact these and other signs indicate that the most able of those who have through haste or conservatism been disposed to ignore dynamical influences in evolution, will before long join in the procession, and lend their undoubted abilities to the perfection and elaboration of the only theory yet propounded which fully and efficiently supplements that of Natural Selection and closes the too obvious gaps which have hitherto existed in the intellectual structure of the modern theory of organic evolution (1890:10).

Osborne (1890) made the same argument in a similar response to the apparent weakening of Weismann's position.

In a review of Dall's paper Jackson (1890a) credited Dall with providing a new way to understand the relationship between dynamic influences and natural selection. Rather than there being two separate forces in evolution, natural selection acted "in harmony with, and as a natural outcome of dynamic influences." According to Jackson, Dall had melded the engine of variation (dynamic influences) with natural selection.

Dall published two other papers that dealt with dynamical influences in molluscan evolution. In the first Dall (1889) addressed the higher classification of the Pelecypoda (Bivalvia). He considered earlier attempts unsuccessful because the characters on which such work had been based were "not fundamental in the evolutionary history of the minor groups" (Dall, 1889:445). For Dall the characters of adductor muscles, gills, and siphons were too variable because they were intimately associated with the "mechanics" of the group. Dall then provided examples to illustrate his point and included a discussion of the role that convergence would play in confusing relationships. Dall regarded the then current classification based on hinge structures as suspect, but he felt it could be resolved if interpreted in the context of dynamical influences as Cope and Ryder had done in their studies of the development of the mammalian foot and tooth.

Dall's "archetypal form of bivalve" was small, with symmetrical, equilateral valves, a short, central ligament, and a smooth hinge area; Dall noted that this was the case in the larval shells of many taxa. He argued for initial small size of bivalves based on the fossil record. Dall also allowed that this condition "in the adult state" was likely due to "degeneration." Thus, as long as the taxa remained small and symmetrical there was no mechanical selection on the hinge structure. However with size increase and/or asymmetry, the forces were no longer trivial and changes in the ligament and hinge plate structure would be compulsory to compensate for the new mechanical conditions: "Nature, through natural selection and physical stresses, has developed these cardinal processes which are known as teeth" (1889:452).

Based on his understanding of the evolution of the bivalve hinge structure Dall proposed three orders. These were the Anomalodesmacea, Priondodesmacea, and Teleodesmacea, the last taxon having the "highest and ev-

olutionarily the most perfect type of hinge." Moreover, "prionodont traces" remained in most members of this latter group, a clear indication of the direction of evolution in these taxa. Dall also correlated the presence of nacre with these tooth types showing it to be common in the Anomalodesmacea, but absent in the Teleodesmacea. The remainder of the paper discussed groupings within these orders and the derivation of their hinge structures. As in his dynamical influences paper (Dall, 1890), he used a supplementary note at the end to again drive home the importance of physical forces in evolution and its implications for reconstructing molluscan evolution. Citing unnamed workers who considered the molluscan shell to be nothing more than a secretion of the mantle, Dall conceded that the "original theoretic protoconch" may have been so, but once it existed it came under the influences of physical forces that influenced the growth and structure of the viscera. Dall saw molluscan anatomy molded by the shell as much as the shell was secreted by a portion of that anatomy. In this view the physical factors that produced the shell acted through the shell to constrain the anatomy. Thus, it was Dall's conclusion that when "intelligently studied and properly appreciated" the relationships of the Mollusca were discernible solely through shell characters. The idea that the shell mechanically constrained the viscera was to be revisited in his second paper considering dynamical influences.

In that work Dall (1894) addressed the mechanical causes of folds in gastropod apertures. Dall began with the observation that among fusiform rachiglossate taxa the attachment points for the adductor muscle lay deeper within the shell in those taxa with columellar folds than in those without folds. He then formulated a model in which the gastropod animal consisted of a thin, loose, cone-shaped mantle epidermis in which the relatively solid body cone resided. The adductor muscle attached this dual cone complex to the shell columella. Dall envisioned that when the animal retracted into its shell "the natural diameter" of the mantle cone would exceed the shell volume and the mantle epidermis would therefore wrinkle longitudinally. The strongest folds would be along the columella because "the attachment of the adductor prevents freedom in wrinkling, and the groove of the canal will mechanically induce the first fold in that vicinity." Repeated extension and contraction of the wrinkled surface over the shell would produce plications on the columella and either lirae or teeth on the outer lip of the aperture.

Dall then returned to his earlier observation of the correlation that the attachment points for the adductor muscle lay deeper within the shell in those taxa with columellar folds than in those without folds. Dall explained that taxa with the adductor muscle closer to the aperture would experience less compression of the body complex and therefore fewer wrinkles of the mantle would be produced. The deeper the adductor attachment point, the more compression of the body and more wrinkling, thereby producing more plications. Dall considered this explanation to have "marvelous precision with the results called for . . . based on the dynamical status of the bodies concerned, their motions and secretions" (Dall, 1894: 913). Moreover, the exceptions were readily clarified. For example, species with extensive mantles typically had lirate apertures (e.g., *Oliva* spp., *Cypraea* spp.). Those with extensive mantles but no lirae did not entirely withdraw into their shells (*Harpa* spp., Opisthobranchia).

Unlike his earlier hinge structure paper, this article made no reference to the usefulness of these characters in understanding the evolutionary history of the rachiglossate taxa in which they were expressed. Instead, Dall seemed to view them as constructional artifacts, features that were present only because of the interaction between tissues and coiled shell. It is interesting that nowhere in this paper does Dall use the term "natural selection." In Dall's evolutionary model, natural selection acted "in harmony with, and as a natural outcome of dynamic influences." Although these particular characters were the products of dynamic influences, they remained neutral and were not selected for, most likely because they were too intimately associated with the "mechanics" of the group.

NEO-LAMARCKIANISM IN MOLLUSCAN CLASSIFICATION

Dall had not previously stated any evolutionary philosophy prior to 1877, so the arguments he marshaled in favor of his 1871 and 1876 patellogastropod classification, combined with the five evolutionary articles discussed above, are used here to examine his approach to reconstructing molluscan relationships during the second half of the nineteenth century.

In 1871 Dall published his first "natural" (=evolutionary) classification of a molluscan taxon, treating the Docoglossa; the classification had been read before the Boston Society of Natural History on 19 October 1870. For the next 50 years this arrangement of taxa would remain virtually unchanged in Dall's publications and serves as one of the best examples of Dall's evolutionary reconstructions.

In the "General Remarks" section, Dall (1871) made several statements that underscored parts of his evolutionary perspective at that time. He considered the group to have a "peculiar persistency of immaturity, when compared with other groups of gasteropods [sic]"; for him this trend was especially evident in the shell, radula, and gills. Dall (1871:233) also found "a certain geographical agreement in regard to generic characters which favors the hypothesis of a development of the various forms from a few more simple and more closely allied ancestors." That concept would be more fully developed in 1876, and although Dall believed that this pattern was the

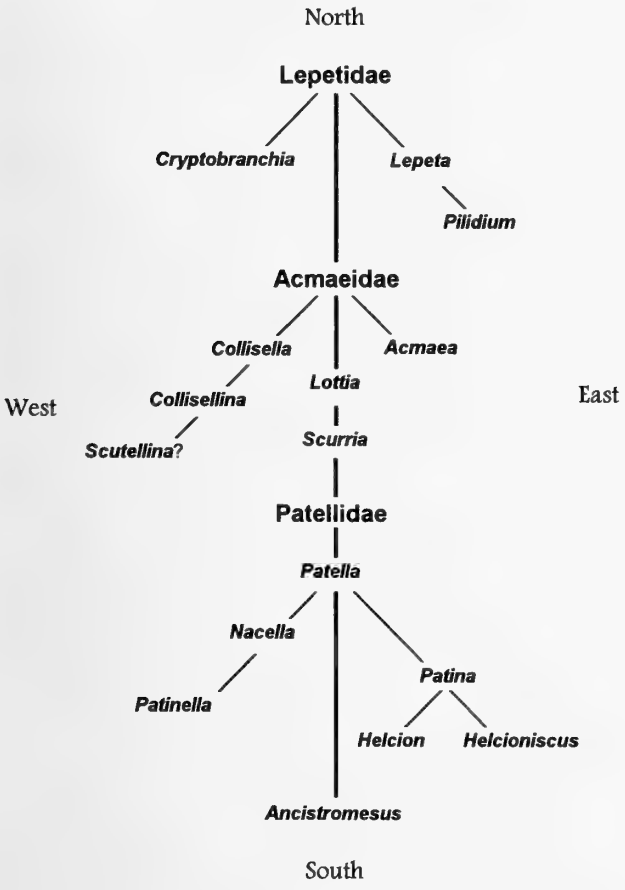

Figure 2

"Genealogical tree" of the Patellogastropoda redrawn from Dall (1876). Note the incorporation of biogeography into Dall's scheme.

result of evolution, he could not attribute it "to the very plausible but highly unsatisfactory doctrine of 'natural selection'."

Dall's (1876) second paper on docoglossan phylogeny began with a comment on Lankester's (1867) mistaken identification of the patellogastropod "wart organs" as gonopores. The anatomical observations that he made to refute Lankester, combined with his acquisition of additional specimens, provided Dall with the opportunity to further resolve and expand upon his earlier phylogeny.

Dall viewed the northwest coast of America as the center of origin of the Docoglossa. From there they had migrated south and east where they "changed or added to their original characters" (Dall, 1876:40) (Figure 2). This pattern required three components to support it: (1) the "maximum development of the lower or parent forms" in the North Pacific, (2) "a local abundance and radiating distribution of the next higher genera," and (3) the presence of the most specialized taxa in the nearest "favorable" region. The importance of the proximity of the "favorable" region was a suspected correlation of time with specialization. Thus, the sooner the ancestral taxon could get to a new area, the more time there would be for subsequent specialization to occur. In the Docoglossans "this is exactly the real state of the case."

Dall considered radula, gills, sensory structures, and body size to be key characters for reading this pattern, and all supported his model. The supposedly most primitive docoglossans, the lepetids, are found subtidally in the Arctic and boreal North Pacific and Atlantic oceans. They are small limpets without eyes, gills, and lateral teeth and are "sluggish in their motions." Given their obviously inferior condition, Dall concluded that they were "protected by the uniform conditions of their deep water station."

Dall suggested that the Acmaeidae evolved from the lepetids by developing the radula (perhaps by "natural selection") and acquiring eyes and gills; a general size increase was also present. "Strong in the possession of their new organs" they invaded the intertidal zone (*Collisella*), although a "few smaller and weaker forms" remained in the subtidal. Traveling westward from their North Pacific center, the Acmaeidae reached Japan (*Collisella*) and migrated down the western Pacific margin to Australia (*Collisellina*). Conditions were less favorable eastward through the Bering Strait and over Arctic Canada, and this accounts for the fact that only two species occur in northern Europe. *Lottia,* with its large size (>100 mm) and the addition of a secondary gill, represented the next step in acmaeid evolution. Completion of the secondary gill along the anterio-most mantle margin in *Scurria* of South America marked the "highest stage of development" in the family.

For Dall the next step in the development of the Docoglossa was the transition from the Acmaeidae to the Patellidae (Figure 2). This was accomplished by (1) loss of the gill from the nuchal cavity ("rejection of useless parts"), (2) development of the muzzle frill into tactile papillae, (3) development of a "rhachidian" [sic] tooth of properly proportioned size, and (4) development of the "abortive uncini of the Acmaeidae" into functional teeth. Moreover, it is in the Patellidae that "the highest development of total bulk known to the order, is added to the greatest known specialization of the other characters."

For Dall there was complete agreement of character polarities and transformations in four distinct character groups of 11 taxa, as well as complete biogeographic congruence between their distributions and relationships as well as aspects of their ecology. These latter two augmentations of character polarization would be formalized as the criterion of "chorological progression" (Hennig, 1966:95). Dall (1876:40) was so confident of his phylogeny that he argued: "In many cases their paths have become dry land, and the track must be followed rather by organic relations than contiguity in distribution." Modern practitioners of vicariance biogeography share Dall's con-

fidence in biological relationships as a guide to reconstructing earth history. Dall knew that "greater knowledge would doubtless increase the complications" for his phylogeny, but he still allowed that "without verging greatly on the speculative, we may construct a genealogical tree, which cannot greatly differ from the following scheme" (Figure 2).

Dall's first two papers on docoglossan phylogeny were published only 5 years apart, but it was 17 years until the third paper appeared. In the interim, all three of Dall's evolutionary theory papers appeared. Dall (1893) wrote the third phylogeny paper as a response to Thiele (1891) whom Dall felt had misinterpreted his conclusions regarding the most primitive members of the Docoglossa. Dall's arguments are similar to his earlier points and there are no obvious references to dynamical evolution. The only element in this paper that may reflect Dall's acceptance of Neo-Lamarckian principles is used as a disclaimer for the phylogeny he was defending. Dall (1893:285) confessed that he attached "little importance to speculations of this kind, which can only be placed on firm footing by extended embryological researches . . ."

After this caveat Dall stated that "we find therefore in Lepetidae the greatest number of archaic characters (somewhat masked by degeneration of other organs) which remain in any of the three groups . . ." (Dall, 1893: 285). To the earlier characters he now added protoconch morphology, and reiterated the patterns of the 1876 phylogeny, starting in the cold north where the simple forms first appeared and subsequently migrated into the temperate and ultimately tropical regions of the world where they became larger and more complex in their character states.

The most interesting portion of this paper is Dall's (1893:287) cautionary remarks about convergence in limpetlike shell morphologies and a prediction about monoplacophoran affinities. A series of discoveries of distinct radular types in deep-sea limpets with virtually identical shells had impressed on Dall the strong convergence that was possible in limpetlike species. If such convergence were possible in living species, fossil taxa would likely present similar problems. Moreover, determinations in the fossil record would be even more dubious, the deeper the time and the more unfamiliar the taxa. He singled out the similarity of shells of Silurian *Tryblidium* with Recent patellid taxa and warned that it was dangerous to conclude that *Tryblidium* anatomy would have been similar to living patellids: "It is almost inconceivable that the Silurian form should have any closely allied recent representative." Moreover, the symmetry of the adductor scars of the monoplacophoran fossils suggested to Dall "a peculiar disposition of the organs which might, indeed, have paralleled in some particulars the organization of some of the *Chitons* of that ancient time." It would be 45 years until the same argument was repeated by Wenz (1938) (see Knight, 1952), and another 19 years before the recovery of living monoplacophorans confirmed Dall's insight into the non-torted state of these animals (Knight & Yochelson, 1958; Lemche & Wingstrand, 1959).

In summary, the overall direction of Dall's evolutionary trends in the patellogastropods was the addition of characters; this resulted in an increase in both complexity and size in descendant taxa. Dall's polarity determinations were based on ingroup comparisons, and by 1893 he thought that the ultimate test of his phylogeny would be made by extended embryological research.

Cladistic analysis (Lindberg & Hedgeaard, 1996) (using many of the same characters that Dall used) produces a hypothesis of relationships that reverses Dall's evolutionary trends and argues that the crown group exhibits mostly paedomorphic, not peramorphic, character transformations (Lindberg, 1988a, b) (*cf.* Figure 1A, B). The diametrically opposed nature of our respective phylogenies results from our different assumptions regarding character polarity and transformations. Dall's model assumed strictly progressive evolution going from simple to complex forms by terminal addition. In contrast, the alternative phylogeny of Lindberg & Hedegaard (1996) is based on a parsimony analysis, with the determination of character polarity and transformations based on outgroup analysis.

Several of Dall's bivalve classifications of the late 1890s and early 1900s also contain terminology and scenarios indicative of Neo-Lamarkian thought. Many of these scenarios contain terms that make them appear mainstream from today's perspective, but dynamic evolutionary thought is clearly present. Dall (1901) considered the shell sculpture of the Lucinacea, which showed virtually no change from the Cretaceous to Recent, to be an example of "neutral selection." Dall argued that the sculpture originally resulted from "trifling mutations of the armature of the mantle edge . . ." but were not "essentials in the lives of these animals . . ." Therefore, once they were acquired "natural selection has little or no influence upon them, and therefore rarely sets up any tendency to change" (Dall, 1901:780).

Dall's (1899) synopsis of the bivalve group "Leptonacea" (= Galeommatacea) well illustrates his evolutionary views at the end of the nineteenth century. He saw in this group the general effects of degeneration overlain by modifications for specific habitats. Dall considered this group to have members representative of "teleodont" ancestors. However, this similarity was only superficial because groups that represented true starting points for taxa are "notable for their tendency to vary and interchange characters." In the Galeommatacea the evolution of commensalism and parasitism produced paedomorphic characters "accompanied by a revival of atavistic primary characters" (Dall, 1899:873). Dental features of the hinge plates of the Galeommatacea resulted from degeneration and had produced indistinct and amorphous dentition.

Bernard (1897) had used positional information to argue homology of bivalve hinge plate structures, but Dall cautioned that:

> The dynamic reactions of the teeth upon each other are, I am confident, of the utmost importance in the development of the hinge. As in the vertebrate skeleton, pressure and friction in localized areas will produce directly a response in facets and buttresses. In fact, to the eye trained to take such matters into account, *every hinge* [emphasis added] shows more or less evidence of the mutability of hinge structure and its responses to stress as well as to inherited tendencies of form (Dall, 1899:874).

Moreover, of all the bivalve groups, Dall thought this mechanism was most obvious in the Galeommatacea. Thus, from a reduced and simplified starting point, "trifling modifications," resulting from dynamical evolution, produced all states seen in the taxon. Although the overall pattern was from simple to complex forms by the addition of structures to the hinge at the pressure points, further degeneration also could occur.

Five of the 17 characters used by Bieler & Mikkelsen (1992) in their phylogenetic analysis of the galeommatacean taxon Galeommatidae were based on hinge structures and all were subsequently discovered to be synapomorphies of clades. Like the patellogastropod example discussed above, most of the transformations in these characters involved reduction or loss (lateral hinge teeth, cardinal teeth), not the simple-to-complex pattern Dall saw in his scheme. Bieler & Mikkelsen also concluded that hinge teeth states were difficult to interpret and score. Unlike Dall, but in agreement with Bernard, they suggested that ontogentic studies would be required to resolve hinge teeth homologies. These and other examples suggest that it was not Dall's eye that was trained to see the natural arrangement of the taxa he studied; it was an unqualified belief in Neo-Lamarckian principles that found its support in every bivalve hinge he examined.

DISCUSSION

William H. Dall's early training in "natural classifications" (see Winsor, 1979), as well as his clandestine exposure to evolutionary theory, began at the Museum of Comparative Zoology (MCZ), Harvard University in 1862. Dall's father, a graduate of Harvard and Harvard Divinity School, took the 17 year old William to meet Louis Agassiz in 1862. Dall subsequently left high school in his final year to begin studies with Agassiz. Although Dall always referred to himself as a "pupil of Agassiz," there is little evidence to indicate that the feeling was mutual. Winsor (1991) does not list Dall as one of Agassiz's students or associates nor does he appear on unpublished lists of students (Winsor, personal communication). Dall's (1908) listing of his fellow students at the MCZ includes J. A. Allen, H. Hagen, C. F. Hartt, F. W. Putnam, S. H. Scudder, and A. E. Verrill and corresponds well with Winsor's student chronology with two notable exceptions. The first is Dall's omission of A. Hyatt who was in residence at MCZ from 1858–1864; the second is Dall's listing of H. Hagen, who did not arrive at Harvard until 1867, 4 years after Dall had left Harvard (Dall, 1908; Winsor, 1991). Dall did not receive a doctorate degree until 1904 when the University of Pennsylvania conferred an honorary degree of Doctor of Science (Dall, 1908).

The absence of W. H. Dall's name from the student rosters likely resulted from the introduction his father provided to Agassiz. The elder Dall was a Unitarian missionary to India and he had hoped to see the younger Dall enter the tea trade in Assam, India. According to Bartsch et al. (1946), Agassiz and his colleagues recognized the potential of having a MCZ collector in India and gave the young Dall intensive training in collecting and natural history. Thus Dall may have had a different curriculum and status at MCZ than his contemporaries. Dall (1908) recounts that his year or so at the MCZ consisted of training in zoology under Agassiz, training in anatomy and medicine under Wyman, and geology from Agassiz's lectures. It is also likely that Dall was exposed to discussions of Darwinian evolution which first began among Agassiz's students (including Morse, Verrill, and Hyatt) in 1860 (Wayman, 1942; Winsor, 1991).

Further zoological training, and especially exposure to evolutionary thinking, were probably limited after Dall left Harvard and the MCZ in 1863. Upon leaving Harvard, Dall did garrison duty at the Watertown Arsenal, then worked on the India Wharf as an office boy for the firm of Deshon & Yarrington (West African Traders), and later that year went to Chicago where he found work in the land office of the Illinois Central Railroad (Dall, 1908). In early 1864 Col. J. W. Foster, aware of Dall's training with Agassiz, asked Dall to serve as his assistant, surveying iron deposits in northern Michigan during the summer of 1864. Upon his return from the field, Dall spent the fall and winter preparing field reports and working on the chemistry of iron and steel. In late 1864 and early 1865, Dall volunteered evenings at the Chicago Academy of Sciences (directed by Robert Kennicott) and studied anatomy and medicine under the direction of Daniel Brainard and N. S. Davis (Dall, 1908).

In early 1865 Kennicott asked Dall to join the Alaska Survey Party for the Russian-American Telegraph Company. He left for Alaska in March 1865 and did not return to the East Coast until October of 1868. Scientific interactions during this time were limited to an 8-month stay in San Francisco between November 1865 and July 1866.

Dall took up residence at the Smithsonian Institution in December 1868 and began working on his collections from Alaska. He had completed his studies for the natural classification of the Patellogastropoda by October 1870.

In July 1871 he was again sailing to Alaska, this time in the employment of the U.S. Coast Survey, and charged with surveying the Alaskan coastline; he returned to the Smithsonian in the winter of 1874 (Woodring, 1958).

After his return he may have discussed some aspects of evolutionary theory with A. Hyatt. In a letter to Dall dated 21 October 1873, Hyatt wrote of the "little successes" Hyatt had experienced on his recent trip to Europe. Hyatt confided to Dall that his "theoretical views with regard to the evolution of forms etc. must undergo great changes but that in the main they are correct." Hyatt did not go into detail in his letter but promised Dall "all sorts of discussions" when he visited Hyatt in Cambridge the following spring (Hyatt, 1873); there is no record of what they may have discussed. Within 3 years of his return, Dall published his paper on saltatory evolution.

The above chronology suggests that Dall had few opportunities to discuss and interact with colleagues engaged in evolutionary studies after he left Harvard until he returned to the Smithsonian in late 1874. Possible exceptions include the time he spent at the California Academy of Sciences and the 3 years at the Smithsonian between 1868 and 1871.

The importance of Dall's contributions to Neo-Lamarckian theory are difficult to gauge. Jackson (1890a) favorably reviewed Dall's paper on dynamical influences in the *American Naturalist* and cited his contributions to molluscan evolution in his work on bivalve phylogeny (Jackson, 1890b). Hyatt (1894) acknowledged Dall only for loaning ammonites to him in his 1894 tome on the *Phylogeny of an Acquired Characteristic.* In contrast, the work and contributions of Cope, Jackson, and Beecher were widely cited by Hyatt. Cope (1896) listed Dall second in research featuring the inheritance of mechanically acquired characters in the Mollusca (Hyatt, Dall, Jackson, and Beecher) and cited Dall's work an additional four times in his text. Kellogg (1908) presented Dall's (1877a) theory of sudden species changes in his chapter on "other theories of species-forming."

Pfeifer (1965), who considered Dall a lesser figure in the American Neo-Lamarckian school, also cited Dall's (1877a) paper, finding in it the Neo-Lamarckian disposition to view evolution as a struggle between the forces of change and those of equilibrium, but there are no other clues here that Dall was writing from a Neo-Lamarckian perspective. To the contrary, he evoked only natural selection as a process, and did not spare his praise of "Mr. Darwin, whom nothing escapes . . ." This paper contains no reference to the inheritance of acquired characters or the source of variation. Instead he attempts to explain statis in the fossil record and argues the equal importance of the "inherited tendency to equilibrium" with the "inherited tendency to vary."

Hyatt's (1877a) accusatory letter that Dall had failed to cite pertinent literature suggests that Dall was not fully immersed in the Neo-Lamarckian literature at that time, and there is evidence that Cope et al. did not consider him one of their own either. Cope's (1896:528) "List of Papers by American Authors who have Contributed to the Evidence Used in this Book" lists Dall's evolutionary papers beginning in 1889. The only reference to an earlier paper is Cope's mention of Dall's (1877b) brachiopod work in which Dall rejected progressive evolution as an evolutionary mechanism in the formation of species pairs, an uncharacteristic action for a supposed Neo-Lamarckian. Lastly, Dall's (1877a) own footnote states that he did not have a copy of Cope's (1868) paper and had not read it since its publication. It had been published 9 years earlier and most likely came out during his 8-month association with the California Academy of Sciences between Alaskan cruises. This suggests Dall was not fully familiar with the literature on evolutionary theory. However, by 1882 there is no doubt of Dall's knowledge of, and membership in the Neo-Lamarckian school (see above).

Dall's account of his formal training, combined with his opportunity to interact with colleagues in the Neo-Lamarckian movement and the above analyses of the evolutionary scenarios in his papers, suggests two stages in Dall's evolutionary thinking. Before 1877 Dall's views were built exclusively around heterochronic processes and often incorporated biogeography into his patterns (e.g., Figure 2). While there were some gestures to the role of natural selection, they were never developed and no alternative evolutionary modes were proposed or discussed. By 1882 Dall had formalized his heterochronic arguments with the patterns of acceleration and retardation espoused by Cope and Hyatt. This is also when examples and arguments in favor of the origination of structures by physical forces and the inheritance of acquired characters first appeared in his writings. Dall's first stage required nothing more than the training he received from Agassiz or reading Agassiz's (1857) "Essay on Classification" (see Winsor, 1991 on the training of Agassiz's students). The influences for the second stage of Dall's evolutionary views most likely came from Hyatt and Cope and developed after Dall returned to the Smithsonian in the late 1870s. Perhaps this was spurred, in part, by Hyatt's review of Dall's (1877a) first evolutionary paper. Interestingly, that paper is primarily Darwinian and therefore anomalous to both stages.

It is likely that Dall's role and involvement in the American Neo-Lamarckian movement has not been widely recognized in malacological circles because his prodigious publication record has caused the few primarily evolutionary articles to be lost among the hundreds of papers on other topics. Moreover, most of his biographers have been malacologists who have focused on his contributions to molluscan systematics rather than his views on evolution. For example, Woodring (1958) in a biography for the National Academy of Sciences listed Dall's "principal contributions to science," but not a single publication on evolution is listed. I think there is little doubt

that if dynamical evolution had not been rejected as an evolutionary hypothesis, Dall's contributions in this area would have been prominently listed here. Dall bet on the wrong horse, and although his evolutionary philosophy had tremendous implications for his systematics and ultimately the classifications he produced, it has been previously ignored because of a paradigm shift.

It is both unfair and inappropriate to judge Dall's evolutionary thinking in terms of today's theories and assumptions of evolutionary processes and models. For their time Dall's evolutionary arguments are both plausible and internally consistent. With the rediscovery of Mendel's work in the early twentieth century and the emergence of a new model for the passing of characters between generations and the origin of variation, the Neo-Lamarckian model was no longer viable and its advocates were soon quiet.

Although criticism of Dall's evolutionary theories is untimely, the legacy of his immense contribution to North American molluscan classification *based on those theories* remains like a skeleton in the closet. Because of the nomenclatural status of his work, and because nomenclature and taxonomy are not decoupled, it cannot be swept away or ignored as a silly idea of the past. Dall's evolutionary model determined how he evaluated character state polarities, transformations, and their import. In his monographs and revisions he ordered his species and higher taxa from "primitive" to "derived," reflecting his best interpretation of their "natural order." The recognition of Dall's intent and the rules by which he interpreted history requires us to carefully consider the implications of following his classifications today. The necessity of using phylogenies in biological or paleontological studies that purport to draw evolutionary conclusions is well documented (e.g., Lauder, 1990; Brooks & McLennan, 1991; Wenzel, 1992; Padian et al., 1994). While criticizing Dall may be inappropriate, workers who continue to use his classifications in evolutionary studies without first rigorously testing his phylogenies do not share his exemption.

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THE VELIGER

Distribution and Reproductive Biology of *Sepietta neglecta* (Naef, 1916) (Cephalopoda: Sepioidea) in the North Aegean Sea (Eastern Mediterranean)

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Abstract. *Sepietta neglecta* (Naef, 1916) is the most rarely caught species of the genus *Sepietta* (Sepiolidae). Its presence in the North Aegean Sea (Eastern Mediterranean) is recorded for the first time, on the basis of 56 specimens, collected at depths from 24 to 262 m, during six seasonal trawl surveys carried out from September 1992 to December 1992. Specimens were dissected, weighed, and assigned a maturity stage. The weight-length relationship was found to be allometric. Mature individuals were caught during all six cruises. In mature males, from 150 to 240 spermatophores were counted, whereas in females, up to 127 oocytes were counted of which only a fraction (6–36%) were in the last stage of development. The ovaries of mature females contained oocytes at three vitellogenetic stages: primary oogonia, maturing oocytes, and smooth ripe oocytes ready to be released. The diameter of ripe occytes, in the major axis, ranged from 1.4 to 2.8 mm.

INTRODUCTION

Sepietta neglecta (Naef, 1916) is a small, nectobenthic species with a maximum mantle length of about 30 mm. It is found in the Mediterranean Sea and on the coasts of the Eastern Atlantic from the southern coasts of Norway (Wirz, 1958) to Morocco (Guerra, 1992). Although it was described by Naef as early as 1916, it is very rarely caught, in contrast to the other two species of the genus *Sepietta* (*S. oweniana* [d'Orbigny, 1840] and *S. obscura* [Naef, 1916]). Its presence in the Eastern Mediterranean (east of 23°E) was doubtful (Digby, 1949) until 1972 when one male specimen was identified by G. Ruby & J. Knudsen, in Cyprus waters. More recently, it was recorded in the Sea of Marmara (Katagan et al., 1993). The present records represent the first occurrence of *Sepietta neglecta* in Greek waters. Most of the published records of *Sepietta neglecta* concern males, perhaps because of the great resemblance of females to those of *Sepietta oweniana* (Naef, 1923), which does not ensure the identification of the species unless individuals of both sexes are found. Very little information on the biology of this species is available in the literature. Its embryonic and post-embryonic development to a final mantle length of 15 mm has been studied by Boletzky et al. (1971) by rearing animals in the aquarium, from eggs collected from bivalve shells trawled off Banyuls-sur-Mer, France (Western Mediterranean). The present report contributes to the knowledge of the biology of this species by giving some information on length-weight relationships, maturity stages, and oocyte size frequencies in mature females.

MATERIALS AND METHODS

Fifty-six specimens of *Sepietta neglecta* were caught from trawlable bottoms in the North Aegean Sea (Figure 1) during six seasonal cruises in 1992–1993. A commercial trawler of 115 tons gross tonnage, equipped with twin 250 Hp engines, echosounder, radar, and plotter, was hired. The trawl used was a nylon net with a cod-end mesh of 16 mm from knot to knot. The bottom area investigated was subdivided into four depth strata: 0–50 m, 50–100 m, 100–200 m, 200–500 m; and the sampling was based on random-stratified design. The minimum and maximum depths trawled were 16 m and 416 m, respectively. For each trawl survey, 65 hauls, ranging from 45 min to 60 min in duration, were performed.

The specimens of *Sepietta neglecta*, together with other sepiolids found during the surveys, were preserved in 5% formalin. They were identified in the laboratory under a dissecting microscope, according to the suggestions of Naef (1923), i.e., mainly by observing the hectocotylized arm of the males and, for the females, by comparing the tentacle and tentacular club sizes with those of equally large *Sepietta oweniana*, which have longer and more robust tentacles.

For 48 specimens, dorsal mantle length (DML, mm) and weight (gr) were measured; sex and stage of maturity of the gonads (Lipinski, 1979) were assessed. Oocytes

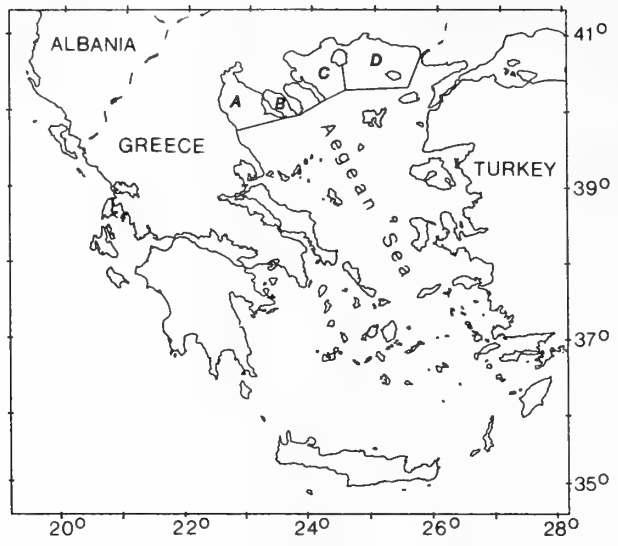

Figure 1

Sampling areas in the North Aegean Sea. A: Thermaikos Gulf; B: Toroneos Gulf; C: Strymonikos Gulf; D: Thracian Sea.

and spermatophores were counted in 10 mature females and eight males, respectively. Development of the oocytes of *Sepietta neglecta* was divided into three stages: (I) primary oogonia, (II) maturing oocytes, reticulated by invading follicular epithelium, and (III) smooth ripe oocytes ready to be released. Ooocyte lengths (longest dimension) were measured for each stage, to the nearest 0.01 mm with an ocular micrometer in a stereoscope.

RESULTS

The 48 specimens examined are listed in Table 1, indicating geographical zone, date of capture, depth of the station, dorsal mantle length and weight of the individuals, and maturity stage of their gonads.

Sepietta neglecta was found in all the subareas on sand-muddy bottoms, sometimes covered by Crinoidea, and at depths ranging from 24 m to 262 m. Together with this sepiolid, other cephalopods were found that have a wide bathymetrical distribution, like *Sepietta oweniana, Sepiola rondeleti* (Leach, 1817), *Rondeletiola minor* (Waef, 1912), *Alloteuthis media* (Linnaeus, 1758), *Illex coindetii* (Vérany, 1839), *Eledone cirrosa* (Lamarck, 1798), *Sepia orbignyana* (Férussac, 1826), and *Sepia elegans* (Blainville, 1827). *Loligo vulgaris* (Lamarck, 1798), *Octopus vulgaris* (Cuvier, 1797), and *Eledone moschata* (Lamarck, 1798) were also found together with *Sepietta neglecta* in shallower stations.

Dorsal mantle lengths ranged from 12 mm to 23 mm for females and from 13 mm to 23 mm for males (fixed specimens). Mature individuals were caught throughout the year. Minimum spawning sizes were 16 mm DML in the male and 15 mm DML in the female. In mature males

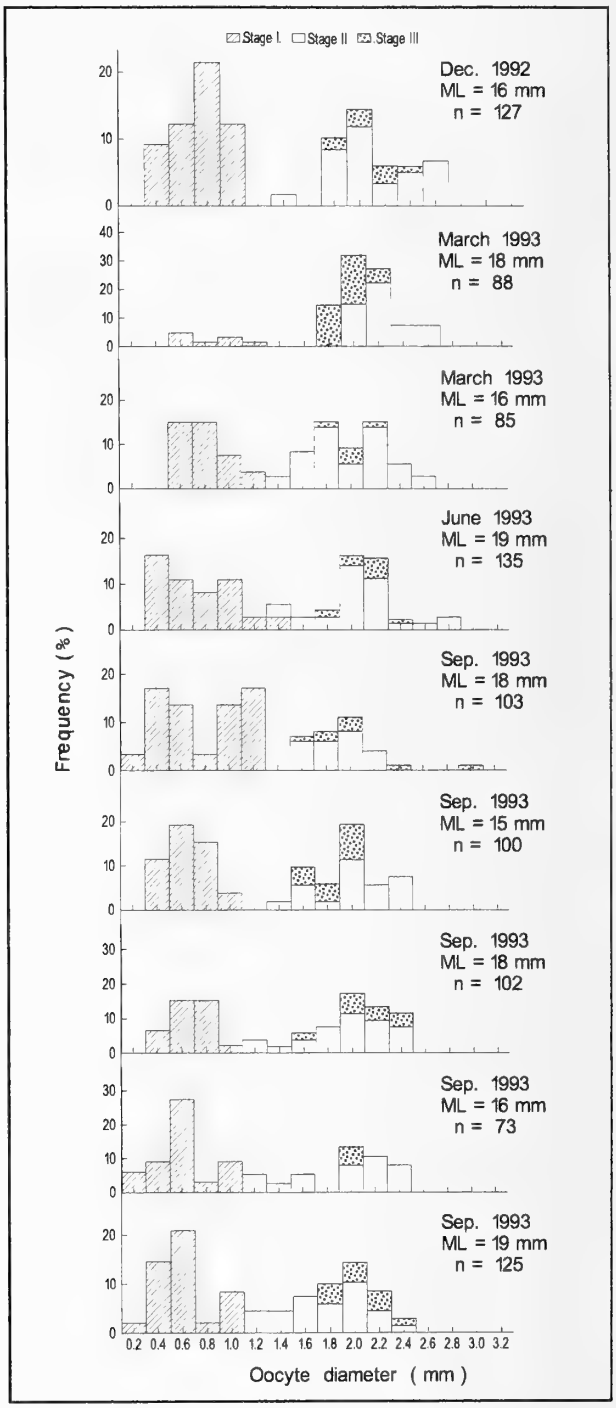

Figure 2

Frequency distribution of oocyte diameter (longest dimension) of three vitellogenic oocyte stages in ovaries of mature (stage IV–V) *Sepietta neglecta* collected seasonally in the North Aegean Sea. Each panel represents the ovary from one female.

Table 1

List of specimens of *Sepietta neglecta* caught during six trawl surveys carried out in the North Aegean sea from 1992 to 1993, with indication of fishing zone, depth, individual size (in mm DML), weight (in gr) and maturity stage in both females and males. A = Thermaikos Gulf; B = Toroneos Gulf; C = Strymonikos Gulf; D = Thracian Sea.

			Females			Males		
Date	Depth (m)	Zone	DML (mm)	Weight (gr)	Maturity stage	DML (mm)	Weight (gr)	Maturity stage
29 Aug. 92	66	A	15.5	2.9	III	19.4	2.4	V
						17.5	1.5	V
07 Dec. 92	73	C	18.0	3.5	VI	13.0	1.5	IV
						18.8	3.8	V
						18.0	2.8	IV
08 Dec. 92	115	C	16.7	2.0	IV	16.0	2.7	V
						18.9	2.7	V
						18.5	2.4	V
08 Mar. 93	262	B	18.0	2.2	V			
			16.0	2.4	IV			
09 Mar. 93	167	B	13.0	1.5	IV	18.0	2.3	V
			15.0	2.4	IV	21.0	2.7	V
12 Mar. 93	115	C	22.1	2.8	V	23.0	3.6	V
			16.0	1.8	V	17.0	2.6	IV
			19.0	2.8	V			
14 Mar. 93	136	C	17.4	2.1	V	15.0	1.7	II
			13.0	1.1	III			
			12.0	1.3	IV			
04 Jun. 93	102	A				19.0	2.4	III
05 Jun. 93	71	A	21.0	3.5	V	15.0	1.9	II
						18.0	1.8	
						18.0	2.9	
04 Sep. 93	229	A	15.0	1.7	V	14.0	1.7	
			18.0	2.1	IV	15.0	1.5	II
						17.0	2.1	
						17.0	2.3	IV
						13.0	1.2	
08 Sep. 93	79	C	16.0	2.1	IV	15.0	1.6	IV
			19.0	1.9	V			
			23.0	3.4	V			
			17.0	1.9	V			
			18.0	2.7	V			
			17.4	2.5	V			
			16.3	2.1	V			
12 Sep. 93	80	D				19.0	2.3	IV
17 Dec. 93	24	D				22.0	3.2	

(Lipinski stage IV), from 150 to 240 spermatophores were found, the maximum length of which was 5.9 mm. Maximum oocyte count in the ovaries of 10 mature (Lipinski stages IV, V) females was 127. However, only a fraction of the ova, ranging from 6% to 36%, were in the last stage of development. The ovaries contained oocytes at all three stages. Size frequencies of the oocytes in nine mature females are presented in Figure 2. The maximum diameter of oocytes ranged from 0.1 to 1.2 mm in stage I, from 1.2 to 2.75 mm in the stage II, and from 1.4 to 2.83 mm for the smooth oocytes at stage III.

A least square regression equation was calculated from the logarithmically transformed dorsal mantle length (DML, mm) and body weight (W, gr) data, pooling both sexes given the small number of individuals available. The resulting power function was:

$$W = 0.000285 * ML^{1.528} \quad r^2 = 0.614$$

from which the allometric nature of the growth of *Sepietta neglecta* can be recognized.

DISCUSSION

The records of *Sepietta neglecta* in the North Aegean Sea confirm the wide distribution of the species in the Mediterranean Sea. The bathymetric distribution in the North Aegean Sea does not seem to be correlated with sex, as far as our data suggest. The species was found from in-

fralittoral to bathyal grounds, as was expected from other records in Cyprus waters: 135 m (Ruby & Knudsen, 1972), in the Gulf of Cadiz: 70–475 m (Guerra, 1982), in the Adriatic Sea: 30–200 m (Bello & Motolese, 1983; Guescini & Manfrin, 1986), off Taragona: 315–363 m (Sanchez & Morales, 1986), in the Ligurian Sea: 30–300 m (Relini & Bertuletti, 1989), in the Sea of Marmara: 50–140 (Katagan et al., 1993), and in the Strait of Sicily: 86–335 (Jereb & Di Stefano, 1995).

The presence of mature animals in every season indicates continuous spawning throughout the year, as observed by Relini & Bertuletti (1989). However, because of the small number of individuals caught and the lack of samples in intermediate months, it is not possible to define a peak or a pause of spawning.

In the ovaries of females ready to spawn, as in other cephalopods of small size (Mangold, 1987), only a fraction of the total number of ova are mature at any one time. Therefore, fecundity estimates are misleading; one does not know the number of eggs that can mature during a prolonged spawning period (Gabel-Deickert, 1995)

The low number of eggs produced by mature females may reflect a reproductive strategy also adopted by other species of cephalopods (Caddy, 1983). Large yolky eggs under maternal protection would provide better chances of survival of the young individuals than is the case in many marine fish species.

The maximum oocyte diameter is similar to that noted by Relini & Bertuletti (1989). It has to be mentioned, however, that some oocytes in stage III were found to have smaller diameters than others in stage II, which means that oocytes, after the disappearance of follicular folds, may decrease in size. Such observations have been made in other sepiolids too (Lefkaditou, unpublished data). In the major-axis length frequency distribution of eggs in the ovary and oviduct of a mature female of *Illex argentinus* (Rodhouse & Hatfield, 1990), the largest eggs appear in the ovary, which could also enforce this hypothesis.

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THE VELIGER

Reinstatement of *Williamia subspiralis* (Carpenter, 1864) (Gastropoda: Siphonariidae)

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Abstract. The northeastern Pacific siphonariid species *Williamia subspiralis* (Carpenter, 1864), synonymized by Dall (1870) under *W. peltoides* (Carpenter, 1864), is reinstated and a lectotype designated. It differs in its higher profile, more posteriorly projecting apex, and in its narrower distribution and offshore habitat, as shown by ANOVA and discriminant function analysis.

INTRODUCTION

In this paper I demonstrate the existence of a second species of the pulmonate limpet genus *Williamia* Monterosato, 1884, in the northeastern Pacific, differing from the broadly ranging species *Williamia peltoides* (Carpenter, 1864) in its higher profile and more posteriorly projecting and downturned apex. This species, *Williamia subspiralis* (Carpenter, 1864), was briefly proposed in the *Supplementary Report* . . . , in a checklist format (Carpenter, 1864a:650):

> ?*Nacella subspiralis,* n. s. Shaped like *Emarginula rosea,* and may be a *Scutellina.* 10–20 fm. Cp.

It was subsequently more completely described (Carpenter, 1866:213):

> *Nacella subspiralis* Cpr.? n. s. State Collection, 416b
>
> N. t. parvâ, carneâ, laevi, tenuissimâ; vertice "Emarginulae" simulante, subspirali, sed apice patelloideo, adunco; t. aduitâ valde elevatâ; margine laterali antico subrecto, apice, projiciente, valde remoto; postico maxime fornicato; aperturae margine antice et postice prolongato. Long. 0.26, lat. 0.19, alt. 0.20, div. 80°. [Translation: *Nacella* with shell small, flesh-colored, curved, very thin; whorl similar to the "emarginulinids," with low spire, but with apex patelloid, curved; adult shell very elevated, lateral margin anteriorly elevated, projecting apex very far removed, in posterior region extremely curved; margin of aperture anteriorly and posteriorly prolonged]. *Hab.* Catalina Island, 10–20, fm., 4 dead, Cooper. This may be the young of the long-lost *Patella calyptra,* Mart. It may be a *Scutellina.* Even the genus cannot be predicated from the shell alone.

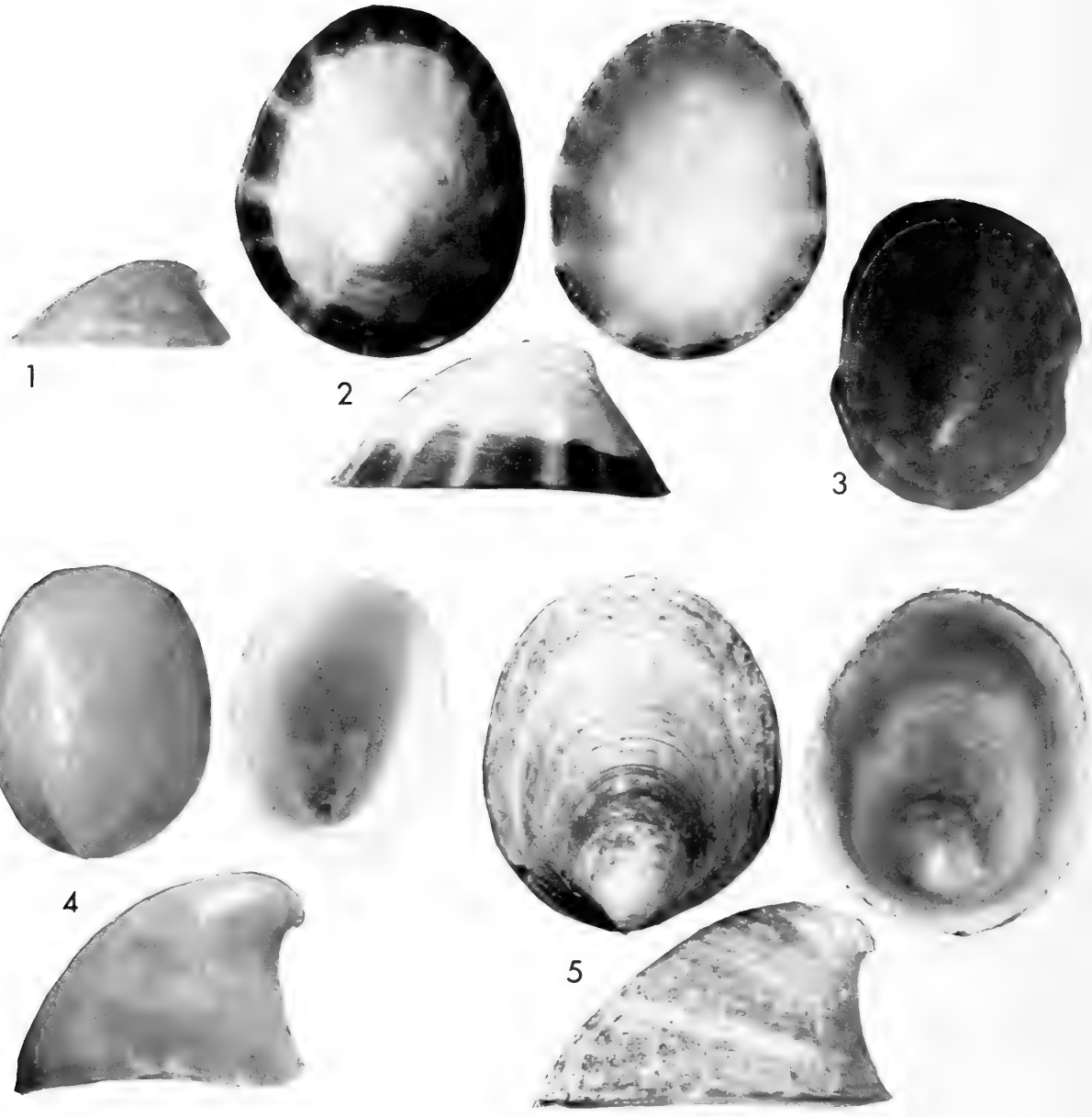
Like all of Carpenter's species, it was not illustrated.

Four years later Dall (1870) recognized it to be a siphonariid limpet, and stated: "study of the type convinces me that it differs from normal adult specimens of [*Siphonaria*] *peltoides* only in being abnormally elevated. . . ." In the same paper Dall (1870) placed in synonymy the name *vernalis,* a manuscript name of his own that he later validated as var. *vernalis* (Dall, 1878). Much later, Dall (1921:67) raised *vernalis* to a full species and listed two northeastern Pacific species in *Bulletin 112: Williamia peltoides* and *W. vernalis.* Dall (1921) published drawings, dorsal and right lateral views, said to be of the "type" of *Williamia peltoides* (Dall, 1921:pl. 15, figs. 10, 12). No catalog number or locality was cited, nor was there any justification for declaring the figure to represent type material. These illustrations, which have been copied by many authors, are now for the first time identified as representing *W. subspiralis.* Four years later, Dall illustrated the holotype of *vernalis* from Monterey, California (Dall, 1925:pl. 27, figs. 3, 5). The latter illustrations show what is now regarded as typical of large specimens of *W. peltoides* from California.

Although Dall (1921) had correctly surmised that there were two northeastern Pacific species, he had both of the names wrong. His treatment of *Williamia peltoides* and its congener *W. subspiralis* over the course of his long career was not indicative of his best work. However, as the following account shows, his successors, including me, were hardly more adept at unraveling the confusion that he created.

Grant & Gale (1931:463) were first to assess the two species indicated by Dall (1921) in *Bulletin 112,* which then were known as the high-profile *peltoides* and the low-profile *vernalis.* They placed *vernalis* in the synonymy of *peltoides,* dismissing the high form figured by Dall: " . . . the higher form with hooked apex being merely a morphological response to the less rigorous habitat on broken shells and small rocks beyond the direct pounding of the surf." This was pure speculation, although they were correct in attributing the high-profile form to deeper water. No mention was made of the Carpenter name *subspiralis.*

Hubendick (1946:71) overlooked Grant & Gale's treatment and followed Dall (1921) in accepting two species



Explanation of Figures 1 to 5

Figures 1–3. *Williamia peltoides* (Carpenter, 1864). Figure 1. Lectotype, USNM 4023; left side, length 4.0 mm (the specimen is still glued on its right side to the original glass slide). Figure 2. Holotype of *Liriola peltoides* var. *vernalis* Dall, 1878, USNM 32596; three views, length 13.3 mm. Figure 3. Holotype of *Williamia galapagana* Dall, 1917, USNM 60417; exterior view, length 9.0 mm. Figures 4–5. *Williamia subspiralis* (Carpenter, 1864). Figure 4. Lectotype, UCMP 39880; three views, length 7.0 mm. Figure 5. LACM 41-76.16, 27–38 m, off Smugglers Cove, Santa Cruz Island, California; three views, length 12.1 mm.

(*vernalis* and *peltoides*), citing the name *subspiralis* under *peltoides,* which he knew only from the Dall (1921) illustration.

Type material for Carpenter's two names was discussed by Palmer (1958). Carpenter's specimen of *peltoides* came from Cape San Lucas, collected by John Xantus. Type material has remained unfigured until now, although Palmer (1958:260) designated a lectotype (USNM 4023), which is an immature specimen of 4 mm length (Figure 1). She recognized that the Dall illustration (1921:pl. 15, figs. 10, 12), which was said to be the "type," was much too large to be of type material described by Carpenter.

At the same time, she figured a "syntype" in the Redpath Museum (Palmer, 1958:pl. 25, figs. 15, 16), which I here identify as a lottiid limpet, because the 4 mm specimen she illustrated has two diverging white rays that are frequent in lottiid limpets but never seen in *Williamia.*

Palmer (1958:260) provided a separate account of Carpenter's name *subspiralis,* in which she copied verbatim the two descriptions quoted above of Carpenter (1864, 1866). The more complete description of 1866 in Latin is first translated above. Palmer dismissed the name *subspiralis* on the authority of Dall (1870). Type material from Catalina Island, collected by Cooper, was said by H. Rehder in a personal communication to Palmer to have "since been lost" at the U.S. National Museum. However, the fact that Carpenter attributed the specimens to the "State Collection," which is now at the University of California, Berkeley, suggested that syntypes be searched there. This led to the discovery of two specimens with a label reading "*Acmaea subspiralis* Cpr., Catalina Island, Cooper Coll." These specimens are here designated lectotype (Figure 4) and paralectotype.

Donohue (1965) devoted an entire paper to deal with the problem of Dall's (1921) figures of the supposed type of *peltoides* and, citing Palmer (1958), agreed that these figures did not represent *W. peltoides.* Despite its mention in Dall (1870) and Palmer (1958), he failed to mention Carpenter's name *subspiralis.* Although he noted that Grant & Gale (1931) had mentioned a "high form" of *W. peltoides,* Donohue (1965:21) concluded: "Just what Dall was illustrating we hesitate to guess." Donohue's paper was written without reference to any museum specimens.

Keen (1958:580, fig. 1033) and again in the second edition of *Seashells of Tropical West America* (Keen, 1971:852, fig. 2425) used the name *peltoides* and also copied Dall's (1921) illustrations of the supposed type of *peltoides,* but in the appendix giving sources (1971:964) she credited the figure to Dall but did not state it to be of type material. She did not mention the name *subspiralis* in 1958. In her text of 1971 she included the following synonyms of *Williamia peltoides:* "*Nacella subspiralis* Carpenter, 1864 [first reviser Dall, 1870]; *N. vernalis* Dall, 1878, and *W. galapagana* Dall, 1917 [nomen nudum as of Dall 1909]."

McLean (1969; revised edition, 1978) provided an original illustration for *Williamia peltoides* and placed *vernalis* (Dall) in synonymy. Carpenter's name *subspiralis* was not mentioned.

Abbott (1974:336) again copied the disputed Dall (1921) figure for *peltoides.* Carpenter's name *subspiralis* was not mentioned.

Every author until now has missed or neglected to reconsider Dall's statement that *subspiralis* represents a form that is "abnormally elevated." Having castigated all my predecessors who wrote on the subject of *Williamia peltoides,* I admit to missing it myself. However, following my first look at the paper by Donohue (1965), I have had a new species in mind for what I now understand to be *W. subspiralis,* having only now taken a closer look at that name during the course of preparation of an illustrated manual of the shell-bearing benthic Gastropoda of the northeastern Pacific.

The objective of this paper is to demonstrate the existence of two species that differ in profile, habitat, and distribution, using the tools of discriminant function analysis. Synonymies for the original proposal of names and synonyms, citations of type specimens and type localities, and diagnoses and distributions for the two species are given in the systematic summary.

MATERIALS AND METHODS

Although large numbers of both species (227 lots of *W. peltoides* and 30 of *W. subspiralis*) are represented in the LACM collection, many of the specimens are relatively small and not collected living, having been recovered as worn shells from sediment samples. For both species, eight large, well-preserved specimens from four different localities per species were measured (Table 1).

Statistical analysis was performed with STATISTICA™ for Macintosh 4.1 (Statsoft, 1994). Single, two and three factor ANOVAs were performed on Length (L), Height (H) to Length (H/L), and Apex Position (A) to Length (A/L); the latter two variables were arcsine transformed to fulfill the requirements of normality (Sokal & Rohlf, 1981; Zar, 1984). A discriminant function analysis was performed on the two size independent ratios, and one adding Length as a third variable.

Abbreviations for museums: LACM, Los Angeles County Museum of Natural History; UCMP, University of California Museum of Paleontology, Berkeley; USNM, National Museum of Natural History, Washington, D.C.

RESULTS

The H/L ratio (ANOVA: $F_{(1, 14)} = 15.36$; $P = 0.0015$), the A/L ratio (ANOVA: $F_{(1,14)} = 11.72$; $P = 0.0041$), and the Length (ANOVA: $F_{(1, 14)} = 7.52$; $P = 0.016$) are significantly different in the two species. The two factor ANOVA for the two size independent ratios is significant (Wilk's Lambda = 0.44; Rao's R = 8.023; $F_{(2, 13)} = 8.02$; $P = 0.0054$). These two variables discriminate significantly between the two species as shown by a discriminant function analysis: 75% of *W. subspiralis* and 87.5% of *W. peltoides* were correctly classified by the two size independent variables. The classification functions are: *W. subpiralis* = 309 arcsine H/L + 236 arcsine A/L − 173; *W. peltoides* = 298 arcsine H/L + 247 arcsine A/L − 162. If shell length is taken into account (Wilk's Lambda = 0.31; Rao's R = 8.97; $F_{(3, 12)} = 8.97$; $P = 0.0022$), then 100% of the specimens are correctly classified, despite Length having less than 0.5% of the weight in the classification function, and the parameter for the size in-

Table 1

Measurements (mm) of large specimens of each species. Apex stands for distance of apex from posterior margin of shell. Ratios are shown as untransformed values.

Specimen no.	Length (L)	Width (W)	Height (H)	Apex (A)	H/L	A/L
Williamia peltoides (n = 8)						
1	13.0	11.4	5.15	3.3	0.40	0.25
2a	14.6	11.8	6.65	3.8	0.46	0.26
2b	13.3	11.2	6.4	2.0	0.48	0.15
2c	12.4	10.3	5.5	3.2	0.44	0.26
3a	9.1	7.3	3.2	2.8	0.35	0.31
3b	7.7	5.9	2.8	1.6	0.36	0.21
4a	9.8	7.4	3.7	2.3	0.38	0.23
4b	9.2	7.5	3.8	1.2	0.41	0.13
Williamia subspiralis (n = 8)						
5a	8.1	6.7	4.8	0.8	0.59	0.10
5b	8.75	7.0	4.7	1.2	0.54	0.14
5c	7.8	6.2	3.5	1.3	0.45	0.17
5d	6.8	5.2	3.2	1.3	0.47	0.19
6a	11.9	10.3	6.85	0.6	0.58	0.05
6b	9.2	8.1	4.7	1.5	0.51	0.16
7	6.05	4.5	4.4	0.5	0.73	0.08
8	6.1	4.8	3.2	0.9	0.52	0.15

Locality data: 1. LACM 144388, Cape Arago, Oregon. 2. LACM 19993, Morro Bay, San Luis Obispo County, California. 3. LACM 65-80.48, Portuguese Bend, Los Angeles County, California. 4. LACM 152366, Laguna Beach, Orange County, California. 5. LACM 88–356.56, 37–55 m off Point Sur, Monterey County, California. 6. LACM 41–75.16, 27–38 m, Smugglers Cove, Santa Cruz Island, California. 7. LACM 68-99.4, 33 m, Sandy Point, Santa Rosa Island, California. 8. LACM 72–117.34, 18–24 m, Isla Natividad, Baja California.

dependent variables being virtually unchanged: *W. subpiralis* = 0.589 length + 305 arcsine H/L + 236 arcsine A/L − 174; *W. peltoides* = 1.46 length + 279 arcsine H/L + 249 arcsine A/L − 167.

DISCUSSION

The results of the discriminant function analysis demonstrate the existence of two separate eastern Pacific species that differ in shell morphology. The shallow occurring *Williamia peltoides* lives in protected habitats on the under surfaces of rocks. Grant & Gale's (1931:463) supposition that the "higher form with hooked apex" is "merely a morphological response to the less rigorous habitat . . . beyond the direct pounding of the surf" is falsified because the shallow water forms do not occur in high energy environments. Although distributions of the two species overlap, there are no records from the same station. *Williamia peltoides* lives in the intertidal and shallow sublittoral to 20 m and *W. subspiralis* lives at depths of 20 m or more.

Species of *Williamia* are few and this is the first account of two species with overlapping distributions. Marshall (1981:491) treated the Indo-Pacific species *W. radiata* (Pease, 1861), for which he recognized a poorly differentiated geographic subspecies *nutata* (Hedley, 1908) in Australia and New Zealand, and mentioned the existence of two others in addition to the Mediterranean type species: *W. krebsi* (Mörch, 1877) in the western Atlantic, and *W. peltoides* in the eastern Pacific. Except for the case detailed here, there are few obvious distinctions among these species.

SYSTEMATIC SUMMARY

Genus *Williamia* Monterosato, 1884

Type species (monotypy): *Ancylus gussonii* O. G. Costa, 1829. Mediterranean.

See Hubendick (1946:70) for remarks on anatomy and Marshall (1981) for treatment of the generic-level nomenclature, and radular and protoconch characters. Yonge (1960:117) described the pallial currents in the mantle cavity of *W. peltoides* (as *vernalis*).

In the taxonomic summaries that follow, catalog numbers, type localities and original dimensions for each taxon are placed in brackets following the initial references.

Williamia peltoides (Carpenter, 1864)

(Figures 1–3)

Nacella peltoides Carpenter, 1864b:474 [previously unfigured lectotype of Palmer, 1958, USNM 4023; type locality, Cape San Lucas, collected by J. Xantus, "long. 0.14, alt. 0.05 poll."; not the Redpath Museum "syntype" figured by Palmer (1958:pl. 25, figs. 15, 16)].

?*Nacella vernalis* Dall MS," Dall, 1870:37 [manuscript name in synonymy of *Siphonaria peltoides*].

Liriola peltoides var. *vernalis* Dall, 1878:70, pl. 2, f. 6; Dall, 1925:pl. 27, figs. 3, 5 [holotype USNM 32596; type locality, Monterey, California, Stearns Collection, length 9.0, height 5.9 mm].

Williamia galapagana Dall, 1909:205 [nomen nudum, to replace *Nacella subspiralis* of Wimmer, 1879].

Williamia galapagana Dall, 1917:382 [previously unfigured holotype USNM 60416, labeled "type, Galápagos Islands"; length 9.0, height 3.5 mm].

Diagnosis: Shell brown with well-marked, lighter colored radial rays; apex posterior, slightly projecting, at one-third to one-fourth shell length from posterior margin, slightly below highest point of shell; shell height 0.35 to 0.48 times shell length (Table 1). Shell length to 14 mm.

Records of *Williamia* from the Galápagos Islands begin with Dall (1909) and the appearance of the name *galapagana* (a *nomen nudum* intended for *Nacella subspiralis* of Wimmer, 1879), followed by enough of a description to validate the name (Dall, 1917:382), but no illustrations. This is another synonym of *W. peltoides.*

Williamia peltoides is common throughout its range; specimens from central California to Oregon reach large

sizes, to lengths of 14 mm, whereas the largest specimens from the tropical Eastern Pacific attain a length of 9 mm.

Distribution: Cape Arago, Coos County, Oregon (LACM 144388) to Isla Lobos Afuera, Peru (LACM 74–6) and the Galápagos Islands. Depth range 0–20 m. There are 227 LACM lots, including 54 lots from the Galápagos Islands. Most of these represent small shells recovered from sediment samples.

Williamia subspiralis (Carpenter, 1864)

(Figures 4, 5)

Nacella subspiralis Carpenter, 1864a:650.—Carpenter, 1866:213 [previously unfigured lectotype here designated, UCMP 39880; length 7.0, height 4.9 mm; paralectotype UCMP 39881; type locality, Santa Catalina Island, California, collected by J. G. Cooper].

Diagnosis: Shell brown with faint, lighter colored, narrow radial rays; often with prominent growth markings of lighter and darker bands marking earlier positions of apertural margin; apex posterior, nearly overhanging posterior margin, well below highest point of shell; shell height 0.45 to 0.73 times shell length (Table 1). Shell length to 12.5 mm.

Williamia subspiralis differs from *W. peltoides* in its higher profile, more posterior, more downturned apex, weaker radial rays, and stronger concentric markings. It occurs in deeper water than does *W. peltoides*. In addition to the lectotype, the largest known specimen is figured herein; the usual size for other large specimens is about 8 mm in length. There is little overlap in shell proportions between the two species (Table 1). Relatively low specimens of *W. subspiralis* may be separated in having a more posterior apex.

Distribution: Point Sur, Monterey County, California (LACM 88–356) to Isla Natividad, Baja California (LACM 72–117). Depth range 15–60 m. There are 30 lots in the LACM collection, of which three were collected living.

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THE VELIGER

The Embryonic Development of the Chokka Squid *Loligo vulgaris reynaudii* d'Orbigny, 1845

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Abstract. The embryonic stages of *Loligo vulgaris reynaudii* were examined throughout their development. Egg strands spawned in the sea off Cape St. Francis, South Africa, were transported to a closed seawater system for incubation. The main experimental batch was incubated at 18°C (SD 1.0°C) with a salinity of approx. 36.00‰ and a photoperiodicity of 12L:12D for 16 to 18 days before hatching. Dorsal mantle lengths of hatchlings ranged from 2.3 to 2.5 mm. The major development patterns were similar to those of *Loligo vulgaris vulgaris* and *Loligo forbesi* (eastern Atlantic Ocean). However, *L. v. reynaudii* had a different (faster) development time and a smaller embryo and hatchling size than its closest relative, *L. v. vulgaris.* Also, it is probable that *L. v. reynaudii* hatchlings have fewer yellow and dark chromatophores than those of *L. v. vulgaris.* This needs to be confirmed with additional research on *L. v. vulgaris.*

INTRODUCTION

Approximately 30 species of squid in the genus *Loligo* Lamarck, 1798, are known to occur in coastal and neritic waters of the world oceans (Nesis, 1987). The systematics of the family Loliginidae still requires substantial work, however. Although there have been some bold attempts to clarify both specific points and more general issues, these have left more questions than provided answers, indicating that this research is in a relatively early stage (Natsukari, 1984; Alexeyev, 1992; Yeatman & Benzie, 1993, 1994; Brierley & Thorpe, 1994; Brierley et al., 1995). Authors who investigated genetics of the group on a comparative basis, point out the fact that the systematics of the group is very complex, with many cryptic species. An effort to describe biology and development of each species in the family therefore may help to resolve problems of relations among various taxa.

Loligo vulgaris reynaudii d'Orbigny, 1845, established as a subspecies of *Loligo vulgaris* Lamarck, 1798 (Augustyn & Grant (1988), is a predominantly western Indian Ocean species distributed in the waters off the southern Cape Coast (10°E to 30°E), at depths ranging from less than 10 m to over 300 m (Augustyn, 1989). In recent years, squid have been targeted in an economically important fishing industry in South Africa, exploited mainly by the jig fishery and concentrated along the eastern Cape coastline in depths of less than 60 m (Augustyn, 1989). Catches from jigging have increased enormously from about 500 t in 1983 to more than 10,000 t in 1989 (Sauer, 1991).

To date, studies have concentrated primarily on the distribution, life cycle and ecology of *L. v. reynaudii* (e.g., Augustyn et al., 1992, 1994; Lipinski, 1992). However, studying processes such as hatching success, recruitment, and mortality assists in a better understanding of the life history and is a prerequisite to the adequate management of the fishery (Augustyn et al., 1992). This study was done primarily as a first step to establish a standardized embryonic development scheme for post cleavage stages of development of *L. v. reynaudii,* under stable environmental conditions. The latter may serve as a precursor to a series of experiments to determine the effect of the environment on egg development.

MATERIALS AND METHODS

Egg strands were collected by SCUBA divers from spawning grounds off St Francis Bay (Figure 1) and transported directly in tanks carrying oxygenated seawater to the University of Port Elizabeth, where they were placed in closed recirculating tank systems for incubation. Environmental rooms were used to keep the air temperature low at 5.5°C (SD 1.0°C). The water was well aerated

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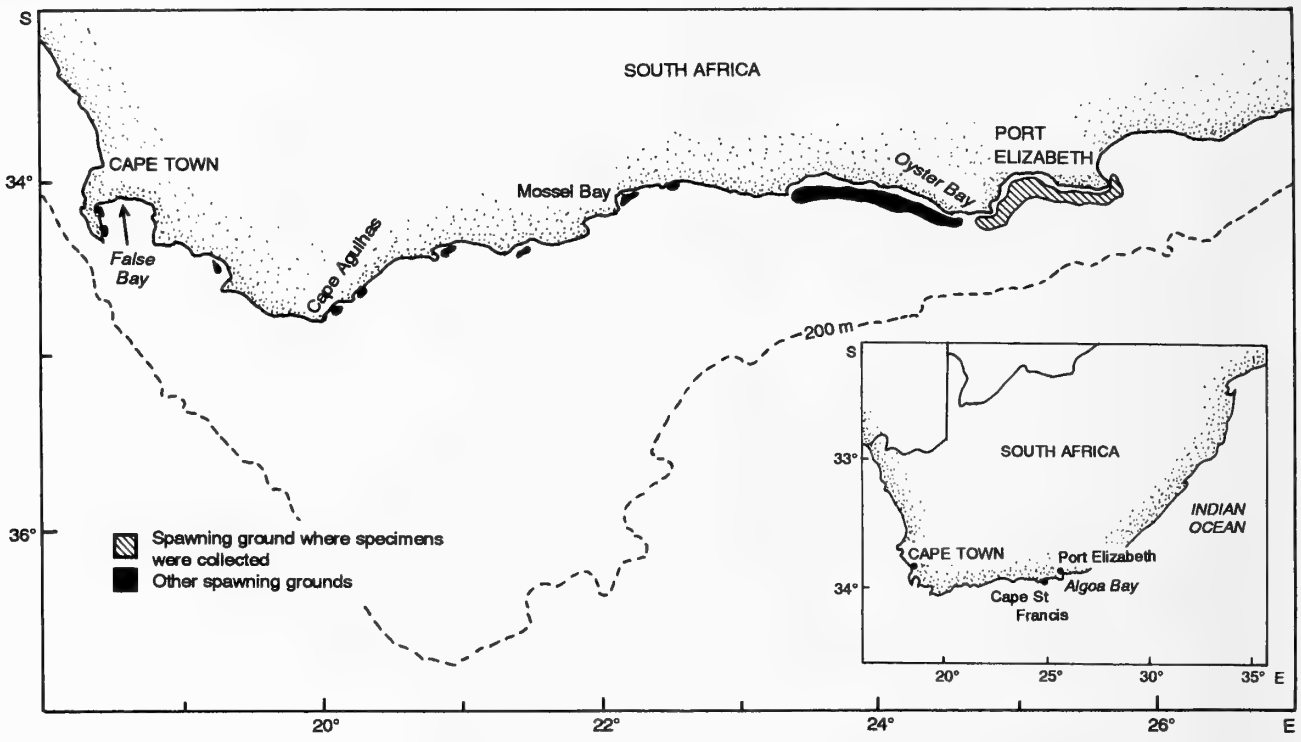

Figure 1

Position of the main spawning grounds of *Loligo vulgaris reynaudii* along the southeast coast of South Africa.

and heated to maintain a mean water temperature of 18°C (SD 1.0°C). The salinity was kept at 36‰ by means of topping up with distilled water.

An egg strand was selected every 24 hours, and carefully examined. A embryo (chosen randomly) was drawn using a 25× magnification stereo microscope and camera lucida. In later stages, the outline was drawn and details added at a 50× magnification. The mantle was also carefully removed to expose the internal organs for inspection. The individual variation between various embryos was not studied in any detail.

All drawings were made from living embryos. Later stages were carefully removed from their egg capsules and suspended in seawater. As their mobility increased with development, ether (bubbled through seawater) was used to render them motionless without causing tissue opaqueness. The survival of embryos investigated in this way was not studied further.

Criteria established by Naef (1928) and Arnold (1965) were used to describe the post-cleavage stages in the embryonic development of *L. v. reynaudii.* Naef's (1928) criteria for *L. v. vulgaris* were used as some resemblance

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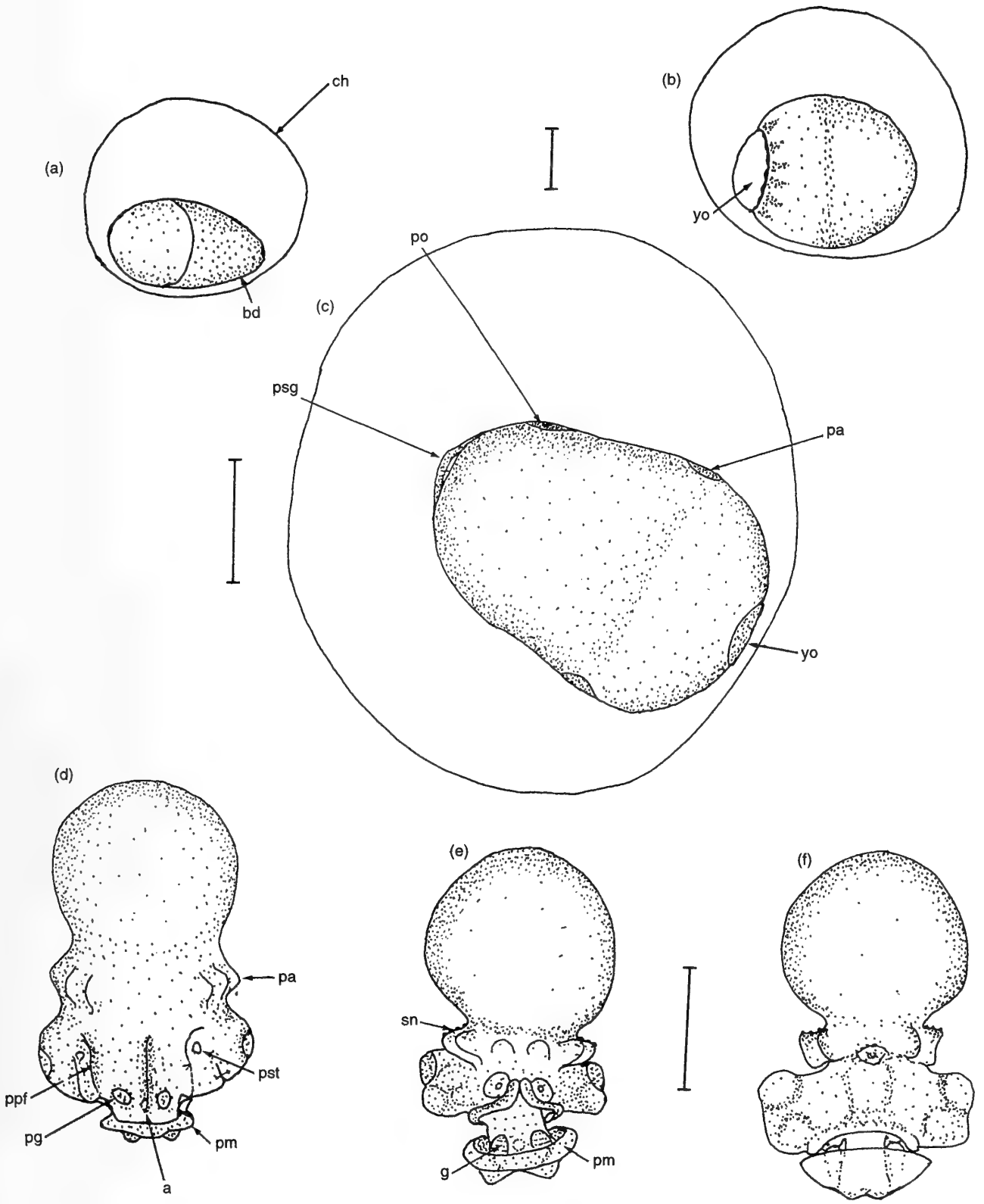
Figure 2

Loligo vulgaris reynaudii: **(a): stage 15 (Arnold) or V (Naef):** Blastoderm covers about one half of the egg. Scale bar: 1 mm; **(b): stage 15+ or VI–VII:** Blastoderm covers four-fifths of the embryo except for a small arc of yolk. A shallow girdling depression appears around the equator, forming a boundary between the future external yolk sac and the future embryonic body. Scale bar: 1 mm; **(c): stages 16–18 (VII):** Nodule of yolk is barely visible. Major organ primordia evident as thickening in the blastoderm. (Primordia of the shell gland are visible). Rudimentary primordia of optic vesicles are visible, and the arm primordia are visible as slight thickening of the blastoderm. Scale bar: 1 mm; **(d): stages 19–20 (VIII–IX):** Primordia of statocysts appear, arms and tentacles grow and begin to project. Posterior and anterior funnel folds extend toward the midline. Shell gland invagination is progressing and transverse fin folds develop on the broadening mantle. Other organ primordia become prominent, such as gills and anal knoll. Scale bar: 1 mm; **(e–f): stages 21–22 (XI–XII):** Shell gland completely closed, transverse fin folds prominent on the developing mantle. Anterior and posterior funnel folds lie together, but fusion of funnel folds has not yet begun. First suckers appear on tentacles. Retina is well pigmented. Scale bar: 1 mm.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was expected, while Arnold's (1965) developmental stages represent a generalized staging system. The Arabic numeral stage represents the stages proposed by Arnold (1965), and the Roman numeral stage represents the stages proposed by Naef (1928). Both ventral and dorsal views are given from Figure 3f onward; before that, only the ventral view was drawn, as the dorsal view did not add substantially more information. The following abbreviated labels were used to describe the most important features; **a,** anal knoll; **ap,** anal papilla; **bd,** blastoderm; **bh,** branchial heart; **bu,** buccal mass; **c,** caecum; **ch,** chorion; **co,** cornea; **ft,** funnel tube; **g,** gill; **h,** Hoyle's organ; **is,** ink sac; **iy,** internal yolk; **l,** lens; **pm,** mantle primordium; **mg,** mid-gut-gland; **op,** olfactory plate; **pa,** arm primordia; **paf,** primordium of anterior funnel fold; **pf,** fin primordium; **pg,** gill primordium; **pl,** lens primordium; **pm,** mantle primordium; **po,** primordium of optic vesicle; **ppf,** primordium of posterior funnel fold; **psg,** primordium of shell gland; **pst,** primordium of statocyst; **sg,** shell gland; **sh,** systemic heart; **sm,** stomach; **st,** statocyst; **su,** sucker; **yo,** yolk. Several additional factors to those reported by Naef (1928) and Arnold (1965) were observed, including chromatophore pattern and internal organ formation (Packard, 1985; Segawa et al., 1988).

To supplement the chromatophore pattern observations in hatchlings, a second batch of eggs was collected in the field (Stage 20–22), transported to Cape Town, and kept in temperatures varying from 19 to 24°C. Squid hatched after 10 days; 21 were observed *in vivo*, and chromatophores counted 1 and 2 days after hatching. In addition, 10 embryos in the last two stages prior to hatching were removed from the egg strands and the change in the number of chromatophores recorded. The method of observation and classification of chromatophores as yellow or dark followed McConathy et al. (1980). All chromatophores observed were tegumental (Sweeney et al., 1992: 3). These were all founder chromatophores according to terminology of Packard (1985) concerning *Octopus,* if this terminology can be applied to loliginid squid.

RESULTS

The egg strands were transparent, gelatinous, fingerlike in shape, and orange in color with the eggs clearly visible. Eggs were wound in a spiral within the egg strand and were ovoid and yolky in appearance. As was described by Augustyn (1989), the color slowly changed to a browner hue during development, and the surface of the egg strands took on a knobbed appearance. Mean egg diameter was 2.8 mm (n = 15).

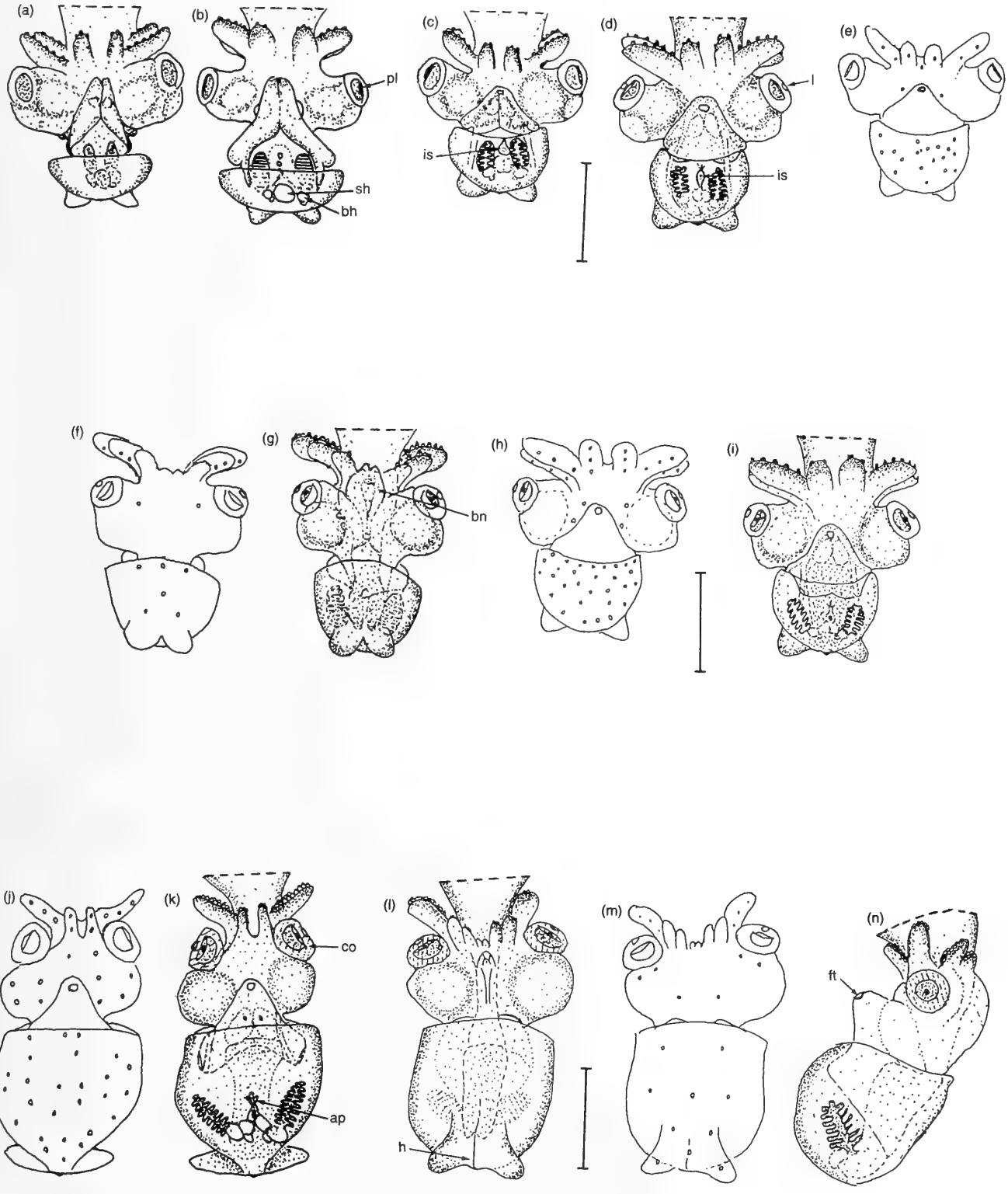
At the onset of the experiment, the eggs were at stage 15 according to Arnold (1965) and at stage V according to Naef (1928). The incubation period was 16 to 18 days at 18°C (SD − 1.0°C). The various stages of development are illustrated in Figures 2–4. The description of each stage is given in the caption of each figure. As stages are often divisible into two or even more steps, some specimens were found to lie between two of the consecutively described stages (denoted by a + or − sign). Although some differences in the developmental processes between those of *L. v. vulgaris* (Naef 1928), *L. pealei* (Arnold, 1965), and *L. v. reynaudii* were observed, Arnold's and Naef's schemes were certainly applicable to the development sequence of *L. v. reynaudii.*

Chromatophores were first observed at stage 26 (XIV) shown in Figure 3e. In almost all cases the first chromatophores were pale yellow in color. Over time (different for individual chromatophores) the color was transformed into a darker red/brown. The chromatophore pattern of a hatchling (chosen at random) is illustrated in Figure 4i, k. Results of individual counts of chromatophores in hatchlings are archived at *The Veliger* FTP site, and a summary of these counts is presented in Table 1.

→

Figure 3

(a): stage 23+ (XI–XII): Suckers first appear on arms III. Mantle begins to grow downward to cover one-half of the gills. Distal edges of the anterior funnel folds are fused. Lens primordia easily visible. Yolk sac separates from the embryo proper. Hearts barely visible through the mantle. Scale bar: 1 mm; **(b): stage 24 (XII):** Retina curved, lenses seen as a refractive rod, funnel folds have formed an anterior opening, the siphon. Mantle continues to grow downward but funnel muscles still evident. Systematic hearts clearly visible. Elongated stomatodeum visible from dorsal view. Scale bar: 1 mm; **(c): stage 25 (XIII):** Mantle covers posterior portion of the funnel but a small triangular opening is still evident, gills completely covered. Individual gill filaments barely visible. Ink sac is visible but no ink is present. Scale bar: 1 mm; **(d–e): stage 26 (XIV):** Pigmentation has begun in the eyes, and ventral chromatophores appear as dark reddish spots. Iris of eye visible as a prominent circle, individual filaments of the gills prominent. Scale bar: 1 mm; **(f–i): stage 27 (XIV–XV):** Dorsal chromatophores present but relatively few in number. Ink is visible in the ink sac. Buccal mass is visible from the dorsal view. Funnel extends to well under the mantle. Secondary cornea begins to cover the eye. Scale bar: 1 mm; **(j–n); stage 27+ (XVI–XVII):** Secondary cornea completely covers the eyes giving a frosted appearance. Organ of Hoyle begins to be prominent dorsally. Ventral arm bases extend into a primary lid and the edge reaches posterior end of eye vesicle. Anus structures clearly visible with conspicuous anal papillae. Chromatophores visibly pulsating, mantle contracting vigorously. Chromatophores appear dorsally on arms II. Scale bar: 1 mm.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A summary of observations made during the last two stages of development is given in Figure 5.

At hatching *L. v. reynaudii* had a mean total length of 4.2 mm and a dorsal mantle length of 2.3 to 2.5 mm (mean 2.4 mm, $n = 41$). A comparison of egg size, hatchling size, and hatchling chromatophore numbers between *L. v. vulgaris* and *L. v. reynaudii* is given in Table 2.

DISCUSSION

Embryonic development has been investigated in detail for only a few species of the genus *Loligo*. Harman & Gardiner (1927) summarized older evidence and provided new material for *Loligo pealei* Lesueur, 1821. Fields (1965) described the embryological development of *L. opalescens* Berry, 1911, but related the development to daily growth (which is highly relative) rather than to a staging system that could be applied over a range of temperatures and development rates. A detailed account of the developmental stages of *Loligo forbesi* Steenstrup, 1856, was given by Segawa et al. (1988). Baeg et al. (1992) described the embryonic stages of *Loligo bleekeri* Keferstein, 1866, under stable environmental conditions. A systematic account devoted to separating hatchlings of *L. v. reynaudii* and *Lolliguncula mercatoris* Adam, 1941, was published by Vecchione & Lipinski (1995).

The speed with which eggs develop in loliginids has been noted to be inversely related to the size of the eggs (Segawa et al., 1988). Yet, in *L. v. reynaudii,* which has large eggs, development was relatively fast; the present experiment indicates an incubation period of 16 to 18 days at 18°C (SD = 1.0°C) from stage 15. This is only 4–6 days longer (from stage 15) than in a comparable group of *Loligo pealei* (Group II of McMahon & Summers, 1971; their fig. 1), which has egg diameters of only 1.0–1.6 mm (after Segawa et al., 1988). For *L. v. vulgaris,* at temperatures of 12 to 14°C, hatching occurs 40 to 45 days after spawning, at 17°C it takes place 30 days after spawning, and at 21°C, 26–27 days would be required (Mangold-Witz, 1963). This would be slightly longer than for *L. v. reynaudii,* taking into consideration the present experiment started at stage 15 and continued for 16–18 days. The size of hatchlings depends largely on the size of the spawned egg (Mangold et al., 1971; Segawa et al., 1988). The eggs of *L. forbesi,* which measure up to 3.1 mm in diameter (Segawa et al., 1988), are the largest known for any loliginid. Egg diameter in other species ranges in size from 2.0–2.7 mm (*L. opalescens*; Fields, 1965), 2.3–2.7 mm (*L. v. vulgaris*; Worms, 1983), and 1.0–1.6 mm (*L. pealei*; Summers, 1983). Therefore, *Loligo v. reynaudii* has relatively large eggs (mean 2.8 mm). The size of hatchlings differs between *L. v. vulgaris* (mean 3.4 mm; Turk et al., 1986) and *L. v. reynaudii* (mean 2.4 mm; present study). In other species of the genus, ML of hatchlings differs widely: from rather small (1.8 mm in *Loligo pealei*; Summers, 1983) through medium size (2.7 mm in *L. opalescens*; Hixon, 1983), to large and very large (3.9–4.9 mm in *L. forbesi*; Hanlon et al., 1989).

The staging criteria suggested by Naef (1928), and improved by Arnold (1965) provide easily recognizable steps, for example, the amount of blastoderm cellulation, eye development (Marthy, 1973), shell gland closure, funnel formation, and the development of the Hoyle's organ. Progressive closure of the optic vesicle, as described for *L. v. vulgaris* (Marthy, 1973) is a good indicator for stages 16–20 (VII–IX). The proportions among some internal organs such as the internal yolk sac, mid-gut gland stomach, caecum, and ink sac change rapidly from stages 28 to 30 (XVII–XX), but their size and position are good staging criteria.

In almost all cases the color of the earliest chromatophores of developing cephalopods are pale yellow. As the chromatpohores age and grow, they are transformed into a darker red-brown color. Floroni (1965) reported such transformations for *L. v. vulgaris,* Packard (1985) for *Octopus vulgaris,* and Segawa et al. (1992) for *Loligo forbesi. Loligo v. reynaudii* is no exception. This progression can be useful in identifying various developmental stages (Packard, 1982). The third (inner row) of founder chromatophores to form on the tentacles at stage 29 (XIX) is an exception to this progression and seems to be a characteristic of loliginid hatchlings (Segawa et al., 1988).

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Figure 4

(a–d): stage 28 (XVIII): Organ of Hoyle is prominent. External yolk sac approximately same size as mantle length. Ink is expelled from ink sac upon agitation. Olfactory plate not yet visible. Mid-gut gland prominently visible dorsally to internal yolk. Yolk is still prominent but mid gut gland is beginning to develop around it. Second row of yellow chromatophores appears on tentacles. Stomach and caecum become visible. Scale bar: 1 mm; **(e–h): stage 29 (XIX):** Third row of chromatophores appears on the tentacles. These are small and red, whereas the second row was yellow. The primordia of the olfactory organ are clearly visible on the ventral head as thickening of the epidermis. External yolk sac approximately equal in length to the tentacle length, it may be lost in cases of premature hatching. Scale bar: 1 mm; **(i–l): stage 30 (XX):** Newly hatched squid. Caecum and stomach increase in size. Chromatophore pattern remains the same as the previous stage until hatching. Hoyle's organ is depleted. Internal yolk sac when viewed ventrally is only visible as a small triangular body surrounded by midgut gland. External yolk sac is discarded or absorbed leaving only a small yolk sac. Scale bar: 1 mm.

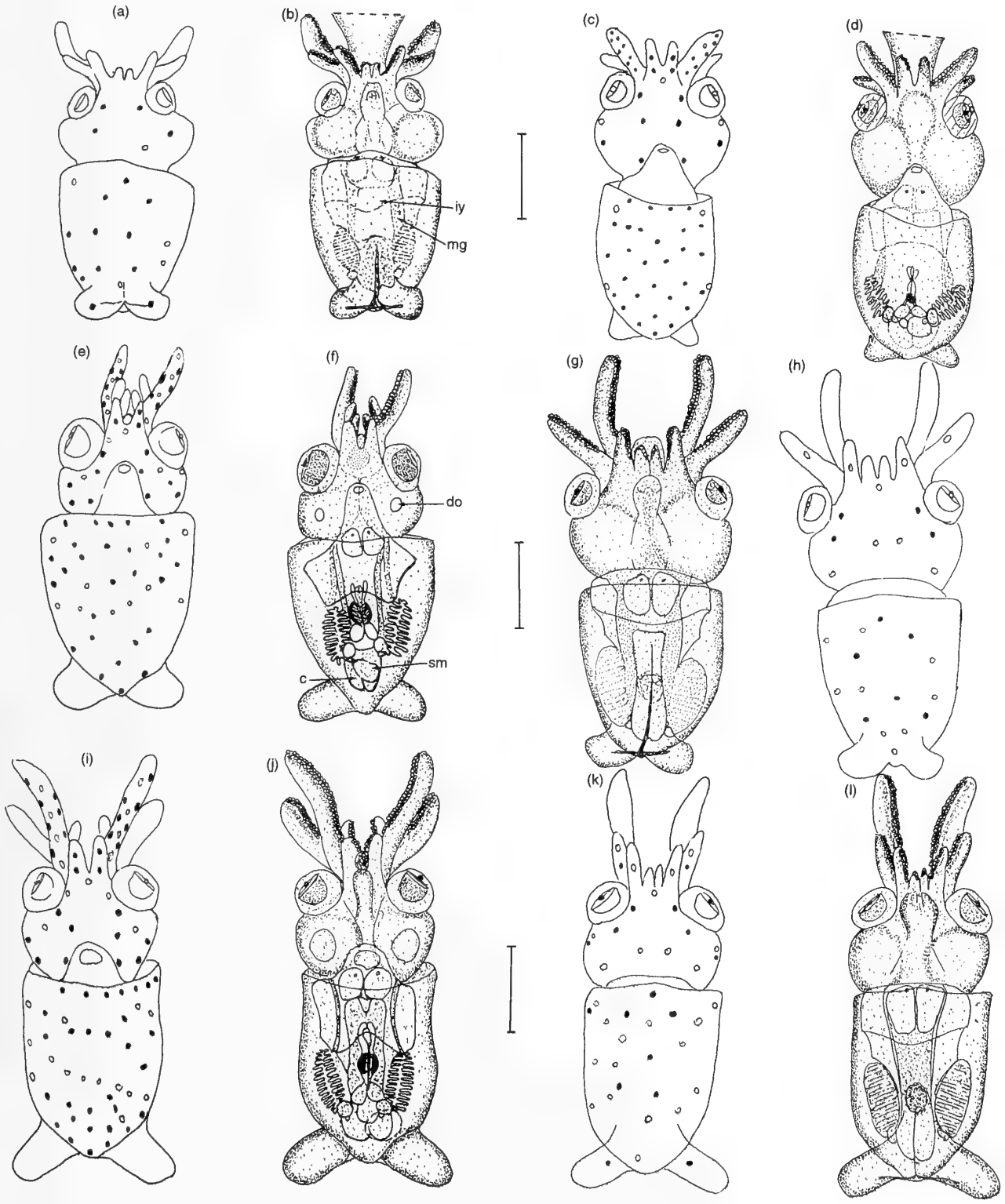
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Table 1

Numbers of chromatophores for 21 hatchlings of *Loligo vulgaris reynaudii* d'Orbigny, 1845; y: yellow chromatophores; d: dark (red or brown). A2–4: arms II–IV pair; T: tentacles; H: head; M: mantle; F: fins.

Characters		Dorsal			Ventral		
		Range	$\bar{x}$	Most numerous class(es)	Range	$\bar{x}$	Most numerous class(es)
A2	y	0–3	2	2	—	—	—
	d	—	0	0			
A3	y	0–4	2	2	—	—	—
	d	0–2	0	0			
A4	y	—	—	—	0–2	0	0
	d				—	4	4
T	y	—	—	—	8–14	11	10, 12
	d				9–15	13*	12, 14
H	y	4–7	6	5, 6	4–8	6	5
	d	4–6	4	4	10–12	11	10
M	y	11–20	15	11, 14, 15, 16	4–14	10	9, 11
	d	4–10	7	6, 7	21–38	31	29, 34
F	y	0–1	0	0	—	—	—
	d	0–3	2	2			

* No individuals with 13 chromatophores.

These were observed to start as small dark reddish spots and once developed, were smaller than the other chromatophores. The chromatophores, (especially those dark red and more readily visible) on the head, arms, and tentacles are one of the best criteria for determining later developmental stages in *L. forbesi* (Segawa et al., 1988), and this was also the case for *L. v. reynaudii.* Because there is considerable variation in the chromatophore pattern on the mantle, the use of the mantle chromatophore pattern as a staging device is not very useful, but still shows how far the embryonic development has progressed in terms of relative density of the chromatophores. In that respect, it appears that *L. v. reynaudii* hatchlings have far fewer yellow and dark (red-brown) chromatophores than *L. v. vulgaris* (Table 2). This is a rather marked difference which may be valid, despite the very small number of observations for *L. v. vulgaris.* A detailed study of the same skin areas of the same individuals during growth (as suggested by Packard, 1982, 1985), coupled with observations of variations between individuals concerning particular chromatophore patterns may be very useful in this regard.

The first drawings of chromatophore patterns in hatchlings (live) and paralarvae (preserved in 4% formalin) of

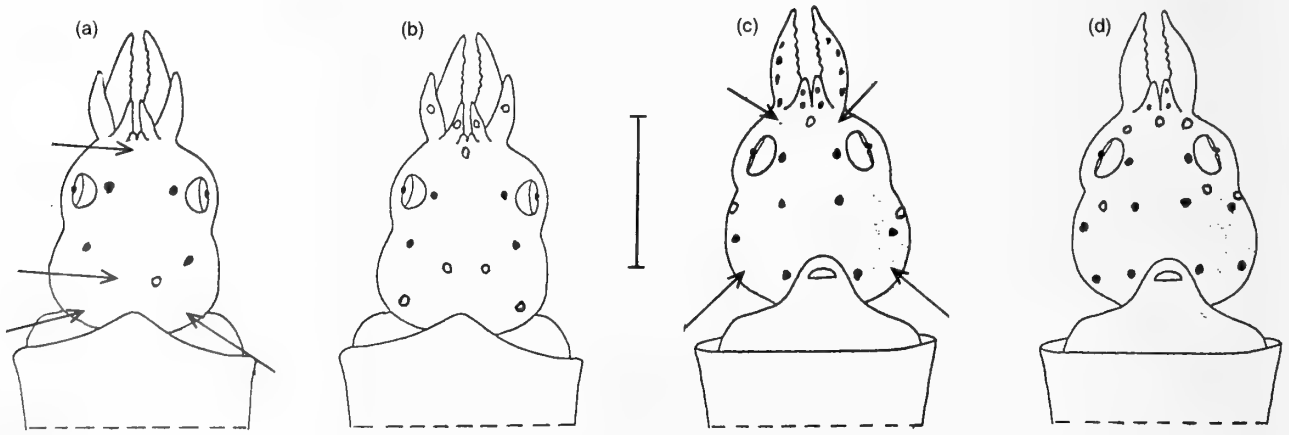

Figure 5

Appearance of some chromatophores of systematic significance between stages **28 (XVIII)** and **29 (XIX)** (arrows indicate missing chromatophores in stage **28 (XVIII).**) Scale bar: 1 mm.

Table 2

The comparison of eggs and hatchlings of *Loligo vulgaris vulgaris* Lamarck, 1798 and *L. v. reynaudii* d'Orbigny, 1845. Abbreviations: see Table 1.

Parameter	*Loligo vulgaris vulgaris*	*Loligo vulgaris reynaudii*
Egg size (mm)	range 2.3–2.7	range 2.6–2.9
	mean unknown	mean 2.8
	n not given	*n* = 15
	(Worms, 1983)	(present paper)
ML (hatching size) (mm)	range 2.9–3.8	range 2.3–2.5
	mean 3.4	mean 2.4
	n large (30 samples)	*n* = 41
	(Turk et al., 1986)	(present paper)
Counts of total hatchling chromatophore numbers ($\bar{x}$)		
Dorsal: A2	4	2
A3	5	2
H	25	10
M	57	21
F	3	2
Ventral: A4	6	4
T	39	24
H	26	16
M	64	41
	n = 2	*n* = 21
	(Hanlon, unpublished)	(present paper)

L. v. reynaudii were presented in Vecchione & Lipinski (1995) and used for identification purposes. There is, however, an important error in fig. 3 (ventral side) of Vecchione & Lipinski (1995). In reality, there is only one pair of dark photophores (most often proximally to the neck) near the eyes of *L. v. reynaudii* hatchling, and not two pairs as shown by Vecchione & Lipinski (1995).

In conclusion, the pattern of chronological appearance of organs in *L. v. reynaudii* is quite similar to that of other loliginids. The considerable homogeneity in the morphological development of loliginid squids has been noted by Hunter & Simon (1975), and recently by Baeg et al (1992). Differences between *L. v. reynaudii* and *L. v. vulgaris* were the rate of development, and the size of the eggs and hatchlings. Differences between chromatophore patterns between the two subspecies are also apparent, although this needs to be confirmed by further study on *L. v. vulgaris.*

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THE VELIGER

Two New Species of *Lampeia* (Bivalvia: Thraciidae) from the Northwestern Pacific, with Notes on *Lampeia adamsi* (MacGinitie, 1959)

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Abstract. The genus *Lampeia* was previously represented in the Chukchi Sea and the northwestern Bering Sea by only one species, *Lampeia adamsi* (MacGinitie, 1959). We found *L. adamsi* in the Sea of Okhotsk at depths of 65–85 m. Additionally, we described two new species from this genus. *Lampeia* ***triangula*** was found in the Sea of Okhotsk off the west coast of Kamchatka at a depth of 144–214 m, *Lampeia* ***posteroresecta*** off the Kurile Islands near Iturup Island at 180 m and in the Fourth Kurile Strait at 500 m. An expanded description of *L. adamsi,* including some additional data on shell morphology, geographic distribution, and habitat is also given.

INTRODUCTION

The genus *Lampeia* (MacGinitie, 1959) was originally described as a new subgenus of the genus *Thracia* Blainville, 1824 (MacGinitie, 1959). Later, this subgenus was elevated by Baxter (1987) to the generic level, still represented only by *Lampeia adamsi* (MacGinitie, 1959) found about 2.5 miles off Point Barrow, Arctic coast of Alaska (MacGinitie, 1959).

For a long time, *L. adamsi* was known only from the Arctic seas. Bernard (1983) did not list it in his catalogue of the living Bivalvia of the eastern Pacific Ocean, in which he listed the species of bivalve mollusks from the Bering Strait (66°N) to Cape Horn (60°S). Baxter (1987) mentioned it only among the fauna of the Chukchi and Beaufort seas. In a detailed review of the contemporary eastern Pacific species of the Thraciidae, Coan (1990) gave the distribution of *L. adamsi* from off Point Barrow westward into the northwestern Bering Sea off Mys Chaplino, Chukotskiy Poluostrov.

No representatives of the genus *Lampeia* have been found previously in the far-eastern and Arctic seas of Russia (Gorbunov, 1952; Golikov & Scarlato, 1977; Scarlato, 1981). As a result of analysis of numerous data on bivalve mollusks collected by many expeditions to the shelf of the western Bering Sea, the Commander Islands, southeastern Kamchatka, the Sea of Okhotsk, and the shelf and bathyal zones of the Kurile Islands, we found material of *Lampeia.* A comparison of our specimens with *L. adamsi* (young and adult specimens) from the northwestern Bering Sea and with the descriptions and photographs of the type specimen (MacGinitie, 1959; Coan, 1990) showed that we found three species. One of the species is *L. adamsi.* This species was found in Russian far-eastern seas for the first time. Two species from our material are new to science. Also, some additional studies of *L. adamsi* from the northwestern part of the Bering Sea were conducted. The purpose of this paper is to describe two new species of the genus *Lampeia* and to give an expanded description of *L. adamsi,* supplemented by new data on its shell morphology, geographic distribution, and habitat.

MATERIALS AND METHODS

In this study the materials on the bivalve mollusks were collected by PRIFO (Pacific Research Institute of Fisheries and Oceanography) expeditions to the Sakhalinsky Bay of the Sea of Okhotsk (R/V *8-452,* 1977) (Figure 1) and to the coastal zone of the western Kamchatka (R/V *Mys Dalny,* 1989 and R/V *Professor Levanidov,* 1996), and a joint Institute of Marine Biology (IMB) PRIFO expedition to the shelf and bathyal zones of the Kurile Islands (R/V *Tikhookeansky,* 1987).

The material from the western Kamchatka was fixed and stored in 4% formaldehyde in the PRIFO. All the other material was stored dry in the IMB.

To separate the material of *Lampeia* into taxa, we used the following characters: proportions and shell shape, lithodesma shape, and peculiarities of shell inner structure. The material of *Lampeia* consisted of both young and adult specimens. A thorough examination revealed distinguishing characters with slight age variability. These diagnostic characters are fairly reliable and allowed us to consider differences in shell morphology among *Lampeia* to be differences on the species level.

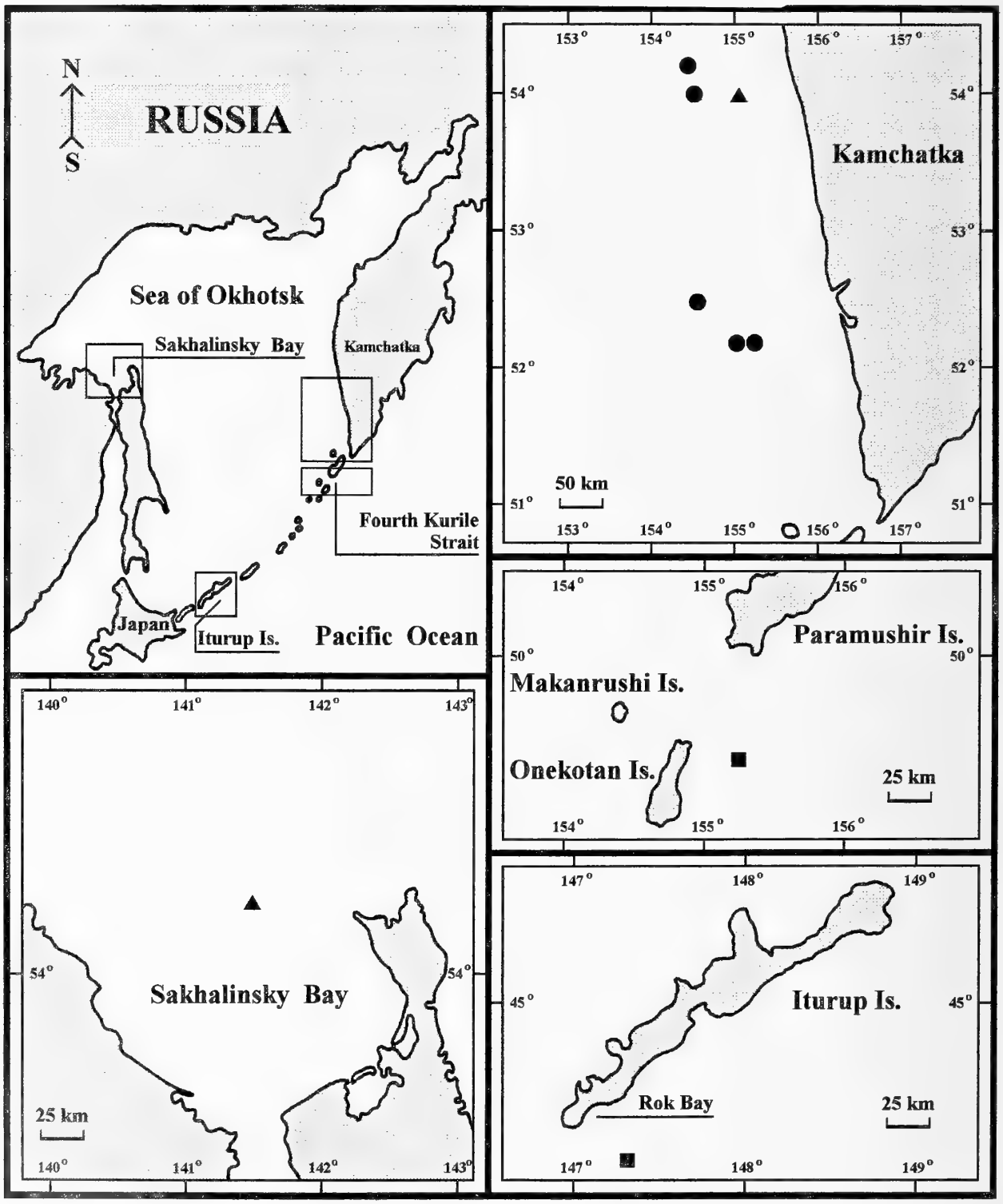

Figure 1

Map showing distributions of *Lampeia* ***triangula*** Kamenev & Nadtochy, sp. nov. (●), *Lampeia* ***posteroresecta*** Kamenev, sp. nov. (■) and *Lampeia adamsi* (MacGinitie, 1959) (▲).

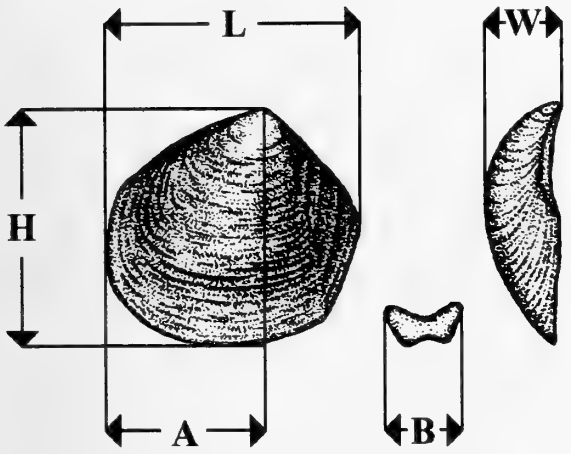

Figure 2

Placement of shell and lithodesma measurements: L—shell length; A—length of anterior end shell; H—height; W—valve width; B—lithodesma length.

Figure 2 shows the position of our shell morphology measurements. Shell length (L), anterior end length (A), height (H), width of each valve (W), length of lithodesma (B) of all the specimens were measured and the ratio of these parameters to shell length (A/L, H/L, W/L, and B/L, correspondingly) were determined. The number of pillars supporting the subumbonal structure for lithodesma in each valve was also recorded. Shell measurements were made using a calipers and an ocular micrometer with an accuracy of 0.1 mm.

The following abbreviations are used: IMB, Institute of Marine Biology, Russian Academy of Sciences, Vladivostok; MIMB, Museum of the Institute of Marine Biology, Vladivostok; PRIFO, Pacific Research Institute of Fisheries and Oceanography, Vladivostok; UAM, University of Alaska Museum, Fairbanks; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington, D.C.

SYSTEMATICS

Family THRACIIDAE Stoliczka, 1870

Lampeia MacGinitie, 1959

Type species (by original designation): *Thracia (Lampeia) adamsi* MacGinitie, 1959; Point Barrow, Arctic coast of Alaska.

Diagnosis: Shell small, inequivalve, truncate posteriorly, covered with a thick brown periostracum. Right valve larger, more inflated. Anterior end longer than posterior. Lunule and escutcheon conspicuous. Ligament both external and internal; external ligament indistinct, represented by a narrow band on dorsal shell margin; main ligament internal, attached to elongate-trigonal structure on shell wall under beaks, extending obliquely posterior from beaks, free along its anteroventral margin, where it is supported by a series of pillars separated by shallow pits. Internal ligament supported by a strong lithodesma. The right valve of some species with a more or less conspicuous toothlike process anterior to the beak on the inner part of anterodorsal margin resembling a true lateral tooth. Pallial line with U-shaped pallial sinus not reaching the midline. Pallial sinus not confluent with pallial line.

Remarks: Coan (1990) showed that the representatives of the genus *Lampeia* have a simple curved lithodesma. An analysis of material of other species shows that the lithodesma shape in representatives of this genus varies greatly and often resembles a butterfly with open wings. One side of it is very curved, corresponding to the form and location of the elongate-trigonal structure on the shell wall, and the opposite side is slightly concave to match the toothlike process on the anterodorsal shell margin, and it partly fits into this depression.

As Coan (1990) noticed, the hinge of this genus is closest to that of *Asthenothaerus* Carpenter, 1864. However, *Asthenothaerus* has no subumbonal structure on the shell wall, supported by pillars. Instead, under the beak, *Asthenothaerus* has a platform for attachment of the ligament and lithodesma. This platform is directed posteriorly, slightly elevated above the inner shell surface and tightly attached to the shell wall. The lithodesma of *Asthenothaerus* is also butterfly-shaped, but it is less massive, more angular, with long, sharp ends, and, in general, has a more complex shape. Species of *Asthenothaerus* also lack an external ligament and have a very thin shell without a thick brown periostracum. They have a thin, tan periostracum.

The hinge of *Lampeia* is also similar to that of *Trigonothracia* Yamamoto, Habe, 1959, which has a small chondrophore and crescentlike lithodesma (Yamamoto & Habe, 1959; Xu, 1980). However, the chondrophore of this genus is directed anteriorly and is not supported by pillars, and the shell is thin and fragile, with a light yellow or brownish periostracum.

We recognized more than one taxon within *Lampeia.* Table 1 describer the main differentiating characters of the three species of *Lampeia.*

Lampeia ***triangula*** Kamenev & Nadtochy, sp. nov.

(Figures 3–23, Table 2)

Diagnosis: Shell high, ovately triangular, twisted posteriorly; beaks high, central or slightly posterior to midline, somewhat sharp, not opisthogyrate; anterior end angular-rounded; posterior end decidedly truncate; anterodorsal and posterodorsal margins straight (sometimes slightly convex), very steeply extending ventrally; posterior margin anteriorly directed; right valve anterior to

Table 1

Some taxonomic characters of the species of *Lampeia*.

Characters	*Lampeia* ***triangula*** Kamenev & Nadtochy, sp. nov.	*Lampeia* ***posteroresecta*** Kamenev, sp. nov.	*Lampeia adamsi* (MacGinitie, 1959)
Shell shape	ovately triangular, twisted posteriorly	ovately quadrangular	ovately subquadrate
Anterior shell end	angular-rounded	rounded	obtusely rounded
Posterior shell end	decidedly truncate	decidedly truncate	broadly subtruncate
Posterodorsal shell margin	straight	concave	straight
Posterior shell margin	anteriorly directed	vertically extending ventrally	anteriorly directed
Beaks	somewhat sharp, not opisthogyrate	slightly rounded, opisthogyrate	rounded, opisthogyrate
Toothlike process on right valve	present	present	absent
Pillars of subumbonal structure	long, wide	long, thin	short, thin
Large pit between anterodorsal shell margin and pillars	absent	absent	present
Lithodesma shape	butterfly-shaped	butterfly-shaped	simple, curved

beak with weakly expressed toothlike process on inner part of anterodorsal margin; pillars supporting subumbonal structure for lithodesma long and wide; lithodesma butterfly-shaped.

Description: *Exterior.* Shell small (to 16.2 mm), high (height almost equal to length), ovately triangular, twisted posteriorly, thick, strong, white under periostracum, slightly inequivalve; right valve slightly higher, sometimes slightly longer, slightly more inflated; periostracum fairly thick, adherent, brown, extending into inner shell surface; surface with conspicuous growth lines, without pustules; beaks central or slightly posterior to mid-line, high, somewhat sharp, not opisthogyrate; anterior end angular-rounded; posterior end decidedly truncate with a faint radial ridge extending from posterior portion of beaks to transition of posterior shell margin to ventral margin; anterodorsal margin straight (sometimes slightly convex), very steeply extending ventrally, forming a very smooth angle at transition to anterior margin; anterior margin slightly curved, rather smoothly transitioning to ventral margin; ventral margin slightly curved; posterodorsal margin straight, very steeply extending ventrally, abruptly transitioning to posterior margin, forming a distinct angle; posterior margin straight, anteriorly directed, forming a smooth angle at transition to ventral margin; lunule present only in left valve, wide, deep, well expressed along entire anterodorsal margin, demarcated by a ridge extending along anterodorsal margin from beaks to anterior margin; escutcheon wide, deep, more expressed in left valve, demarcated by ridges, extending along posterodorsal margin from beaks to dorsal margin.

Interior. Right valve anterior to beak with a small, weakly expressed toothlike process on inner part of anterodorsal margin, often covered with periostracum; in

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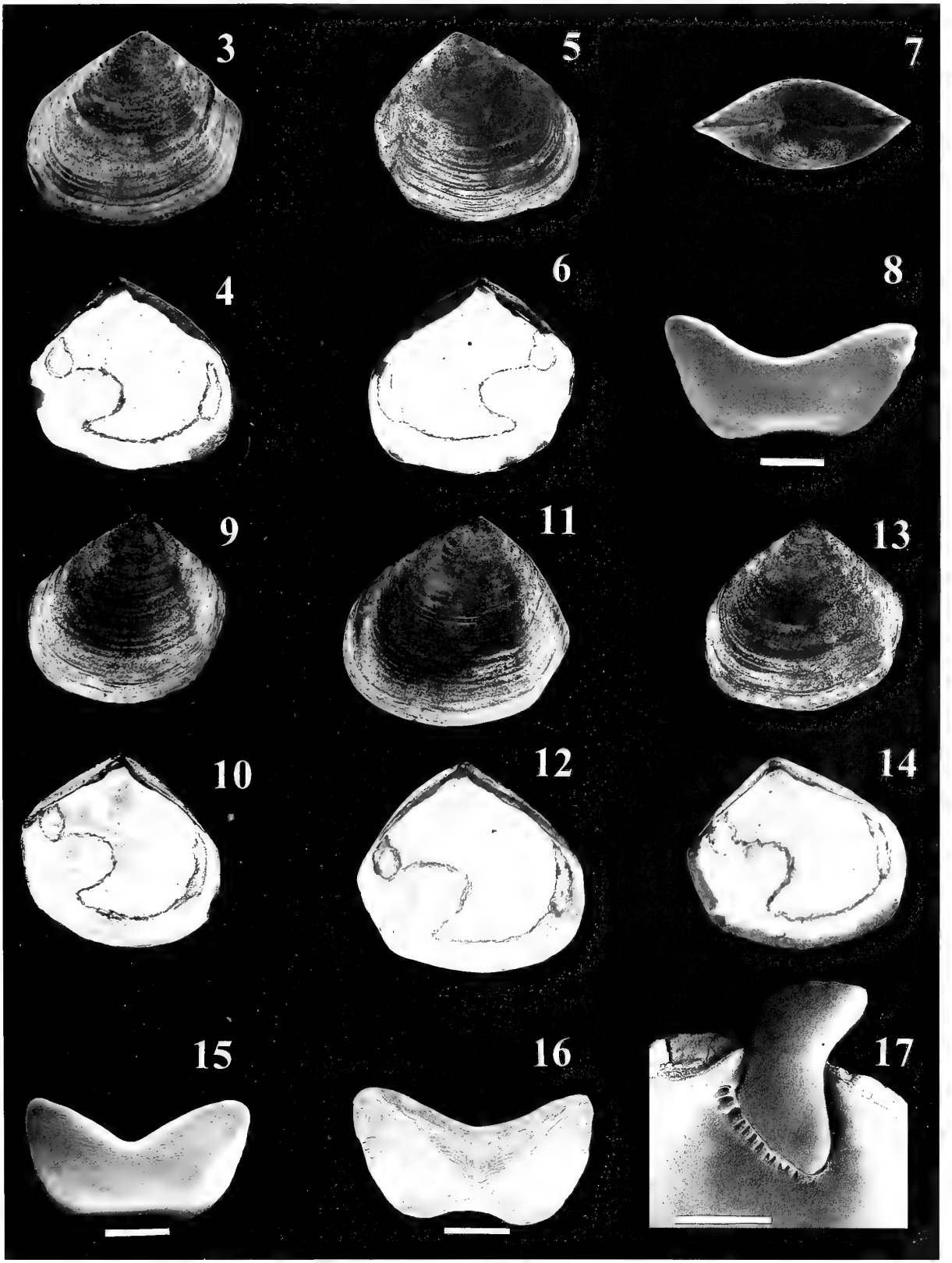
Explanation of Figures 3–17

Lampeia ***triangula*** Kamenev & Nadtochy, sp. nov. Figures 3–8. Holotype (MIMB 1/35169), west coast of Kamchatka, Sea of Okhotsk (52°44′9″, 154°54′5″E), 192 m depth. Figures 3, 4. Left valve, length 16.2 mm. Figures 5, 6. Right valve, length 16.2 mm. Figure 7. Dorsal view of both valves. Figure 8. Ventral view of lithodesma. Scale = 1 mm. Figures 9, 10. Paratype (MIMB 5/35173), west coast of Kamchatka, Sea of Okhotsk (54°20′N, 154°18′E), 144 m depth, left valve, length 15.6 mm. Figures 11, 12. Paratype (MIMB 4/35172), west coast of Kamchatka, Sea of Okhotsk (52°44′9″N, 154°54′5″E), 192 m depth, left valve, length 16.1 mm. Figures 13, 14. Paratype (MIMB 6/35174), west coast of Kamchatka, Sea of Okhotsk (54°20′N, 154°03′6″E), 204 m depth, left valve of a young specimen, length 11.5 mm. Figure 15. Paratype (MIMB 4/35172), west coast of Kamchatka, Sea of Okhotsk (52°44′9″N, 154°54′5″E), 192 m depth. Ventral view of lithodesma. Scale = 1 mm. Figure 16. Paratype (MIMB 5/35173), west coast of Kamchatka, Sea of Okhotsk (54°20′N, 154°18′E), 144 m depth. Dorsal view of lithodesma. Scale = 1 mm. Figure 17. Paratype (MIMB 4/35172), west coast of Kamchatka, Sea of Okhotsk (54°44′9″N, 154°54′5″E), 214 m depth. Close-up of right valve showing the attachment of lithodesma (ventral view) to the buttressed subumbonal structure and the toothlike process on the anterodorsal margin anterior to the beak. Scale = 1 mm.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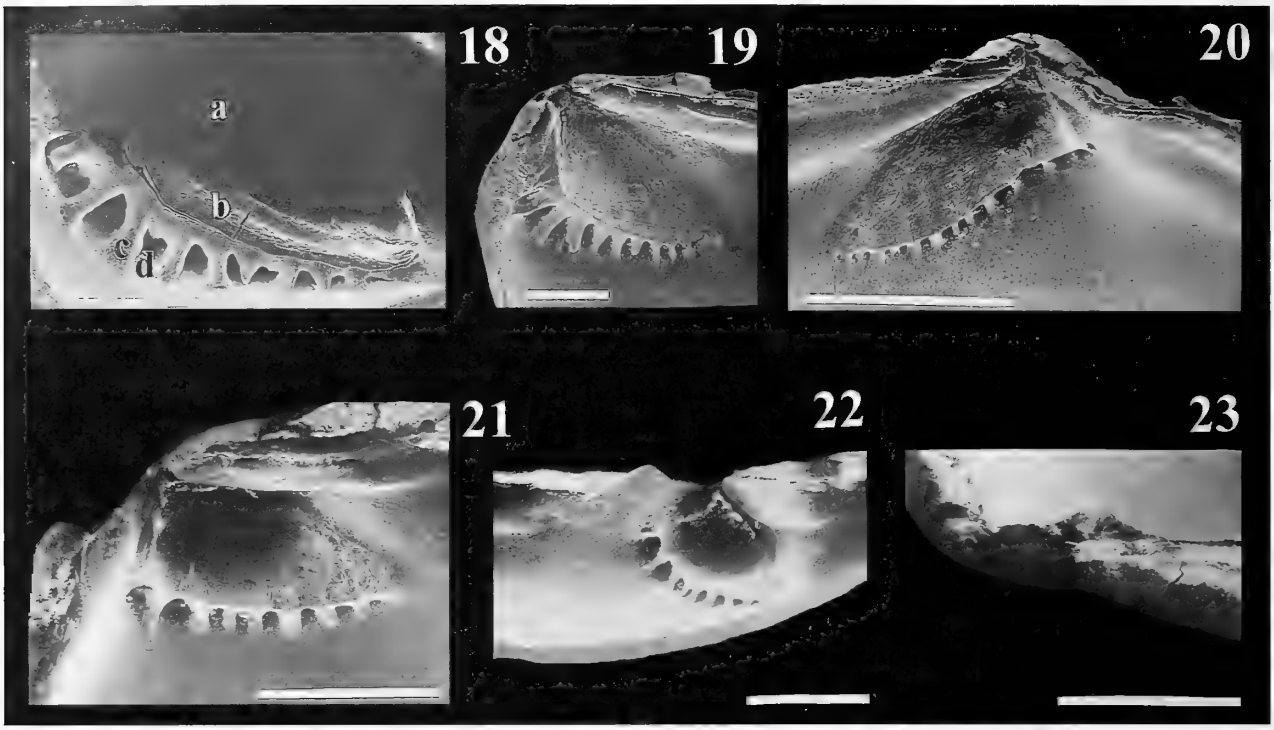

Explanation of Figures 18–23

Lampeia ***triangula*** Kamenev & Nadtochy, sp. nov. Figure 18. Fragment of right valve showing the ligament and pillars of the buttressed subumbonal structure. (a) Lithodesma. (b) Ligament. (c) Pillar. (d) Pit. Scale = 1 mm. Figure 19. Fragment of a right valve showing the buttressed subumbonal structure without ligament. Scale = 1 mm. Figure 20. Paratype (MIMB 4/35172), west coast of Kamchatka, Sea of Okhotsk (54°44′9″N, 154°54′5″E), 214 m depth. Close-up of a left valve showing the buttressed subumbonal structure without ligament and the inner part of the dorsal margin near beak. Scale = 1 mm. Figures 21–23. Paratype (MIMB 6/35174), western coast of Kamchatka, Sea of Okhotsk (54°20′N, 154°03′6″E), 204 m depth. Close-up of a right valve showing the buttressed subumbonal structure without ligament and the toothlike process on the anterodorsal margin. Scale = 1 mm. Figure 21. Interior view. Figure 22. Ventral view. Figure 23. Dorsal view of toothlike process.

left valve anterior to beak; inner part of posterodorsal margin slightly concave; elongate-trigonal subumbonal structure for lithodesma attached to shell wall short; pillars supporting this structure long, in general of the same thickness throughout their length; width of pits between pillars decreasing posteriorly from anterodorsal margin—at anterodorsal margin their width is larger than that of pillars and at posterior they are much smaller; number of pillars varies from eight to 15, lithodesma butterfly-shaped; anterior adductor muscle scar large, elongate; posterior adductor scar large, rounded; pallial sinus medium-sized, broad, of the same shape in both valves, reaching almost to middle of shell, stopping just short of midline; ventral edge of pallial sinus not confluent with pallial line.

Variability: In adult specimens, shell shape and proportions are substantially constant. The shell height-length ratio slightly varies (in the largest specimens height is almost equal to length) (Table 2). Beak sometimes occupies the central position. Anterodorsal and posterodorsal margins are sometimes slightly convex. In young specimens, as compared to adult specimens, shell more elongate, less convex; angles at transition of dorsal margin into anterior and posterior margins and also at their transition into ventral margin are sharper, as a result of which the shell is more angular; beaks sharper, less posteriorly placed, more often central; anterodorsal and posterodorsal margins always straight; length of lithodesma smaller compared to shell length. The relative length of lithodesma increases with age. The shape of lithodesma can vary considerably, but it is always butterfly-shaped. The number of pillars supporting the elongate-trigonal structure varies and is not strongly correlated with shell size.

Type material and locality: Holotype (MIMB 1/35169), west coast of Kamchatka, Sea of Okhotsk (52°44′9″N, 154°54′5″E) (Figure 1), 192 m depth, sandy silt, bottom temperature +0.95°C, Coll. V.A. Nadtochy, 25 July 1989 (R/V *Mys Dalny*). Paratypes (10): Paratypes (3) (MIMB 2/35170), west coast of Kamchatka, Sea of Okhotsk

Table 2

Lampeia ***triangula*** Kamenev & Nadtochy, sp. nov. Shell parameters of the holotype (in italics) and paratypes: L—shell length; A—anterior end length; H—height; W—width; B—lithodesma length; H/L—height–length ratio; A/L—anterior end length–length ratio; W/L—width–length ratio; B/L—lithodesma length–length ratio; N—number of pillars in the buttressed subumbonal structure. Measurements in mm.

Valve	L	A	H	W	B	H/L	A/L	W/L	B/L	N	Depository
Right	9.5	4.7	8.4	1.9	1.6	0.88	0.50	0.20	0.17	13	MIMB
Left	9.5	4.7	8.2	1.7	—	0.86	0.50	0.18	0.17	13	3/35171
Right	10.2	5.3	8.8	2.0	1.6	0.86	0.52	0.20	0.16	10	MIMB
Left	10.1	5.1	8.7	1.9	—	0.86	0.51	0.19	0.16	10	6/35174
Right	10.4	5.5	9.4	2.2	1.7	0.90	0.53	0.21	0.16	13	MIMB
Left	10.4	5.5	9.4	2.1	—	0.90	0.53	0.20	0.16	13	4/35172
Right	10.7	5.8	9.2	2.2	1.7	0.86	0.54	0.21	0.16	14	MIMB
Left	10.7	5.8	9.0	2.1	—	0.84	0.54	0.20	0.16	14	6/35174
Right	11.6	6.0	10.4	2.4	2.0	0.90	0.52	0.21	0.17	8	MIMB
Left	11.5	5.9	10.4	2.3	—	0.90	0.51	0.20	0.17	8	6/35174
Right	12.7	6.5	11.6	2.7	2.5	0.91	0.51	0.21	0.20	10	MIMB
Left	12.6	6.5	11.6	2.6	—	0.92	0.52	0.21	0.21	10	2/35170
Right	14.0	7.0	13.0	3.4	2.8	0.93	0.50	0.24	0.20	13	MIMB
Left	14.0	7.0	13.0	3.2	—	0.93	0.50	0.23	0.20	13	2/35170
Right	14.7	8.5	13.2	3.3	2.8	0.90	0.51	0.22	0.20	15	MIMB
Left	14.7	8.5	13.1	3.0	—	0.89	0.51	0.22	0.20	15	2/35170
Right	15.0	8.3	13.8	3.7	3.3	0.92	0.55	0.25	0.22	11	MIMB
Left	15.0	8.3	13.7	3.4	—	0.91	0.55	0.23	0.22	11	4/35172
Right	15.7	8.6	14.9	3.8	3.6	0.95	0.55	0.24	0.23	12	MIMB
Left	15.6	8.3	14.7	3.4	—	0.94	0.53	0.22	0.23	12	5/35173
Right	*16.2*	*9.0*	*15.2*	*3.7*	*3.4*	*0.94*	*0.56*	*0.23*	*0.21*	*15*	MIMB
Left	*16.2*	*9.0*	*15.1*	*3.3*	—	*0.93*	*0.56*	*0.20*	*0.21*	*15*	1/35169

(54°20′N, 154°30′8″E), 160 m depth, silt sand, Coll. V.A. Nadtochy, 28 July 1989 (R/V *Mys Dalny*); Paratype (MIMB 3/35171), west coast of Kamchatka, Sea of Okhotsk (54°N, 154°33′6″E), 161 m depth, sandy silt, Coll. V.A. Nadtochy, 26 July 1989 (R/V *Mys Dalny*); Paratypes (2) (MIMB 4/35172), west coast of Kamchatka, Sea of Okhotsk (54°44′9″N, 154°54′5″E), 192 and 214 m depth, sandy silt, Coll. V.A. Nadtochy, 25 July 1989 (R/V *Mys Dalny*); Paratype (MIMB 5/35173), west coast of Kamchatka, Sea of Okhotsk (54°20′N, 154°18′E), 144 m depth, sandy silt, Coll. V.A. Nadtochy, 25 July 1989 (R/V *Mys Dalny*); Paratypes (3) (MIMB 6/35174), west coast of Kamchatka, Sea of Okhotsk (54°20′N, 154°03′6″E), 204 m depth, silt sand, Coll. V.A. Nadtochy, 25 July 1989 (R/V *Mys Dalny*).

Other material examined: Five slightly damaged specimens and 1 specimen without detailed label from the type locality.

Distribution and habitat (Figure 1): Known only from type locality.

Comparison: *Lampeia* ***triangula*** differs distinctly from *L. adamsi* in having a ovately triangular shell, a butterfly-shaped lithodesma, and a toothlike process on the anterodorsal margin of the right valve. Externally, ***L. triangula*** (especially young specimens) is most similar to ***L. posteroresecta,*** but has higher beaks that are not opisthogyrate, more steeply sloping anterodorsal and posterodorsal shell margins, a smaller apical angle, anteriorly directed posterior shell margin, more triangular shell shape, wider pillars supporting subumbonal structure for lithodesma and less evident toothlike process on the anterodorsal shell margin.

Etymology: triangular (Latin).

Lampeia ***posteroresecta*** Kamenev, sp. nov.

(Figures 24–38, Table 3)

Diagnosis: Shell high, ovately quadrangular; beaks slightly posterior to mid-line, somewhat rounded, opistogyrate; anterior end rounded; posterior end decidedly truncate; anterodorsal margin slightly convex; posterodorsal margin slightly concave; posterior margin vertically extending ventrally; right valve anterior to beak with a conspicuous toothlike process on inner part of anterodorsal margin; pillars supporting subumbonal structure for lithodesma long and thin; lithodesma butterfly-shaped.

Description: *Exterior.* Shell small (to 20.3 mm), high,

Table 3

Lampeia ***posteroresecta*** Kamenev, sp. nov. Shell parameters of the holotype (in italics) and paratypes: L—shell length; A—anterior end length; H—height; W—width; B—lithodesma length; H/L—height–length ratio; A/L—anterior end length–length ratio; W/L—width–length ratio; B/L—lithodesma length–length ratio; N—number of pillars in the buttressed subumbonal structure. Measurements in mm.

Valve	L	A	H	W	B	H/L	A/L	W/L	B/L	N	Depository
Right	14.8	7.7	13.1	3.6	3.0	0.89	0.52	0.24	0.20	13	MIMB
Left	14.4	7.3	12.8	3.3	—	0.89	0.51	0.23	0.21	13	2/35176
Right	15.7	8.8	14.9	3.7	3.6	0.95	0.56	0.24	0.23	16	MIMB
Left	15.5	8.5	14.3	3.5	—	0.92	0.55	0.23	0.23	16	2/35176
Right	*20.3*	*11.2*	*18.0*	*4.6*	*4.5*	*0.89*	*0.55*	*0.23*	*0.22*	*15*	MIMB
Left	*20.0*	*10.9*	*17.1*	*4.3*	—	*0.86*	*0.55*	*0.22*	*0.23*	*15*	1/35175

ovately quadrangular, thick, strong, white under periostracum, slightly inequivalve; right valve slightly higher, longer, slightly more inflated; periostacum fairly thick, adherent, brown, extending into inner shell surface, in dry shells easily peeling off ventral margin; surface with conspicuous growth lines, without pustules; beaks slightly posterior to mid-line, somewhat rounded, opisthogyrate; anterior end rounded; posterior end decidedly truncate, with a faint radial ridge extending from posterior portion of beaks to transition of posterior shell margin to ventral margin; anterodorsal margin slightly convex, steeply extending ventrally, sometimes forming a very smooth angle at transition to anterior margin; anterior margin slightly curved, smoothly transitioning to ventral margin; ventral margin slightly curved; posterodorsal margin slightly concave, steeply extending ventrally, abruptly transitioning to posterior margin, forming a distinct angle; posterior margin straight, vertically extending ventrally, forming a smooth angle at transition to ventral margin; lunule present only in left valve, wide, deep, well expressed along entire anterodorsal margin, demarcated by a ridge extending along anterodorsal margin from beaks to anterior margin; escutcheon wide, deep, more expressed in left valve, demarcated by ridges, extending along posterodorsal margin from beaks to dorsal margin.

Interior. Right valve anterior to beak with a conspicuous small toothlike process on inner part of anterodorsal margin, not covered with periostracum; in left valve anterior to beak, inner part of anterodorsal margin slightly concave; elongate-trigonal subumbonal structure for lithodesma attached to shell wall rather short; pillars supporting this structure long, rather massive, becoming thinner ventrally; width of pillars approximately equal to width of pits between them; number of pillars varies from 13 to 16; lithodesma butterfly-shaped; anterior adductor muscle scar large, elongate; posterior adductor scar large, rounded; pallial sinus short, broad, of same shape in both valves, not reaching middle of shell, stopping just short of midline; ventral edge of pallial sinus not confluent with pallial line.

Variability: Variability in the proportions of the shell was observed. The shell of one specimen was distinctly higher compared to other specimens (Table 3; MIMB 2/35177). The shape of the shell also varies. In young specimens, the beaks are more prominent, the anterodorsal margin straighter, the anterior end of the shell is more angular because smoothed angles are formed in the transition of the anterodorsal margin to the anterior margin and the anterior margin to the ventral margin. In the largest specimen, the anterior end of the shell is rounded, the anterodorsal margin is slightly convex, and the shape of the shell is close to oval. The number of pillars in the subumbonal structure varies and probably is not greatly de-

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Explanation of Figures 24–38.

Lampeia ***posteroresecta*** Kamenev, sp. nov. Figures 24–29. Holotype, (MIMB 1/35175), Rok Bay, Iturup Island, Kurile Islands (44°11′N, 147°28′6″E), 180 m depth. Figures 24, 25. Left valve, length 20.0 mm. Figures 26, 27. Right valve, length 20.3 mm. Figure 28. Dorsal view of both valves. Figure 29. Ventral view of lithodesma. Scale = 1 mm. Figures 30–35. Paratype (MIMB 2/35176), Fourth Kurile Strait, Kurile Islands (49°38′5″N, 155°22′3″E), 500 m depth. Figures 30, 31. Left valve of a young specimen, length 14.4 mm. Figures 32, 33. Right valve of a young specimen, length 14.8 mm. Figure 34. Dorsal view of both valves of a young specimen. Figure 35. Ventral view of lithodesma. Scale = 1 mm. Figures 36–38. Paratype (MIMB 2/35176), Fourth Kurile Strait, Kurile Islands (49°38′5″N, 155°22′3″E), 500 m depth. Close-up of a right valve showing the buttressed subumbonal structure with ligament and the tooth-like process on the anterodorsal margin. Scale = 1 mm. Figure 36. Interior view. Figure 37. Anteroventral view. Figure 38. Dorsal view of toothlike process.

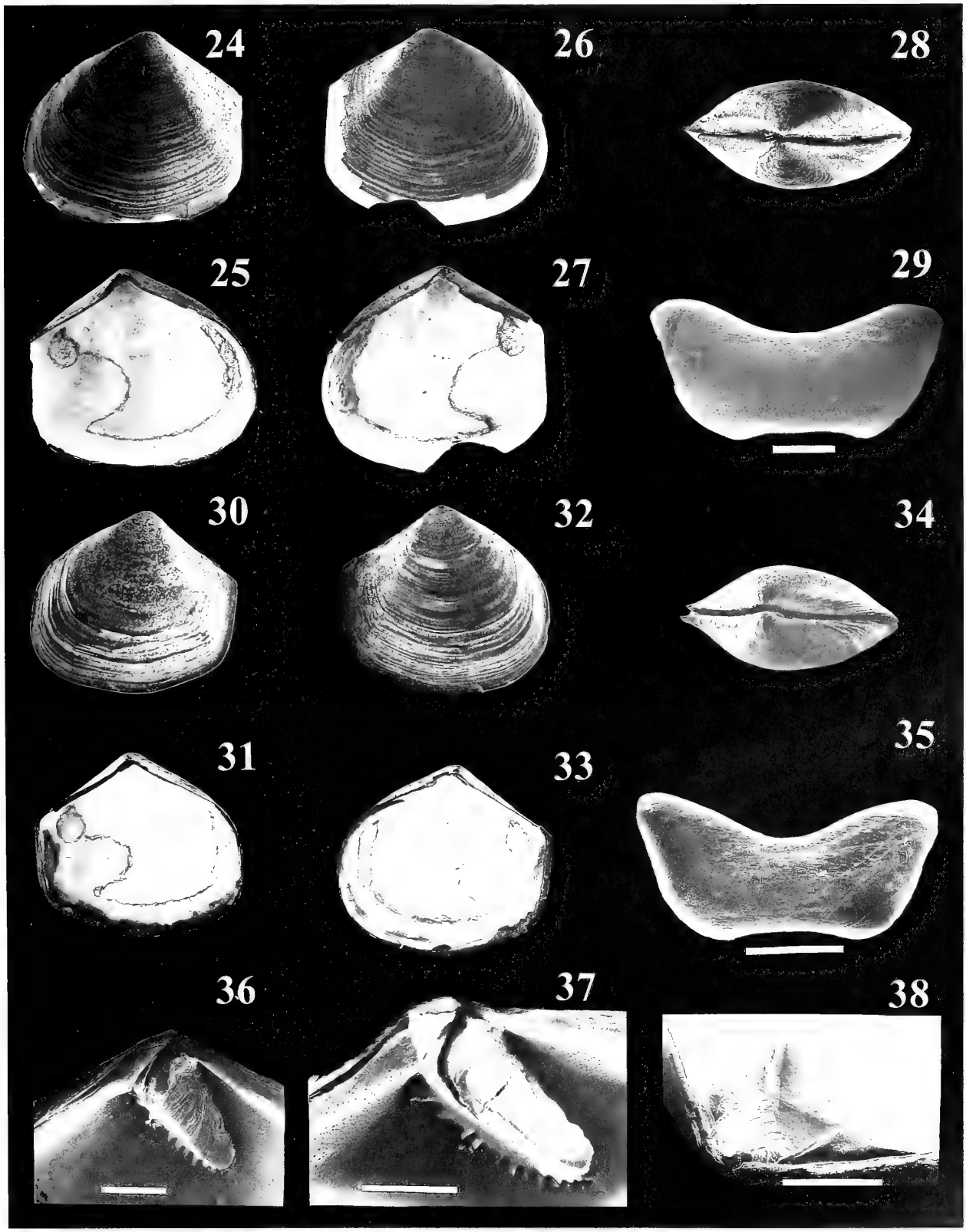
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Table 4

Lampeia adamsi (MacGinitie, 1959). Shell parameters of the holotype (in italics) (MacGinitie, 1959) and specimens from the Sea of Okhotsk (MIMB 1/35177; 2/35178) and the northwestern part of the Bering Sea (UAM 4473): L—shell length; A—anterior end length; H—height; W—width; B—lithodesma length; H/L—height–length ratio; A/L—anterior end length–length ratio; W/L—width–length ratio; B/L—lithodesma length–length ratio; N—number of pillars in the buttressed subumbonal structure. Measurements in mm.

Valve	L	A	H	W	B	H/L	A/L	W/L	B/L	N	Depository
Right	12.6	7.9	10.0	2.5	—	0.80	0.63	0.20	—	13	UAM
Left	—	—	—	—	—	—	—	—	—	—	4473
Right	13.6	8.0	10.4	2.8	—	0.76	0.60	0.20	—	10	UAM
Left	—	—	—	—	—	—	—	—	—	—	4473
Right	15.7	10.3	12.5	3.3	—	0.80	0.66	0.21	—	17	UAM
Left	15.4	10.0	12.1	2.9	—	0.79	0.65	0.19	—	17	4473
Right	16.6	9.2	13.8	3.8	3.7	0.83	0.55	0.23	0.22	15	MIMB
Left	16.3	9.0	13.6	3.0	—	0.83	0.55	0.18	0.23	15	1/35177
Right	*22.8*	—	*18.3*	*6.1*	—	*0.80*	—	*0.26*	—	*15*	USNM
Left	*22.8*	—	*17.3*	*4.4*	—	*0.76*	—	*0.19*	—	*15*	610301
Right	29.7	17.5	25.8	7.7	7.0	0.87	0.59	0.26	0.24	21	UAM
Left	29.1	17.0	24.0	4.9	—	0.82	0.58	0.17	0.24	21	4473
Right	26.7	15.4	21.5	7.1	7.0	0.81	0.58	0.27	0.26	16	MIMB
Left	25.2	14.3	19.8	4.5	—	0.79	0.57	0.18	0.28	16	2/35178

termined by shell size. Some pillars are not attached to the shell wall or are ventrally bifurcated. Lithodesma shape varies but always resembles a butterfly. The lithodesma in larger specimens is longer compared to the shell length.

Type material and locality: Holotype (MIMB 1/35175), Rok Bay, Iturup Island, Kurile Islands (44°11′0″N, 147°28′6″E) (Figure 1), 180 m depth, sand and silt, Coll. V. I. Lukin, 31 July 1987 (R/V *Tikhookeansky*). Paratypes (2) (MIMB 2/35176), the Fourth Kurile Strait, Kurile Islands (49°38′5″N, 155°22′3″E), 500 m depth, sandy silt, Coll. V.I. Lukin and S. I. Grebelny, 27 October 1987 (R/V *Tikhookeansky*).

Distribution and habitat (Figure 1): Known only from type locality.

Comparison: In contrast to other species of the genus, the posterior margin of ***L. posteroresecta*** is vertically directed downward. This species also distinctly differs from *L. adamsi* by having a toothlike process on the inner margin of the anterodorsal margin in the right valve. As compared to the most externally similar species, ***L. triangula,*** ***L. posteroresecta*** also has smaller, somewhat rounded beaks, opisthogyrate, less sharply sloping anterodorsal and posterodorsal shell margins, larger apical angle, shell shape closer to ovately quadrangular than to trigonal, thinner pillars supporting subumbonal structure for lithodesma, more conspicuous toothlike process of the anterodorsal margin of the right valve.

Etymology: Posteriorly truncate (Latin).

Lampeia adamsi (MacGinitie, 1959)

(Figures 39–59, Table 4)

Thracia (Lampeia) adamsi MacGinitie, 1959:163–164, pl. 18, fig. 9; pl. 21, figs. 7, 8; pl. 24, fig. 8; Keen, 1969: 850–851, fig. F27, 8a–d.

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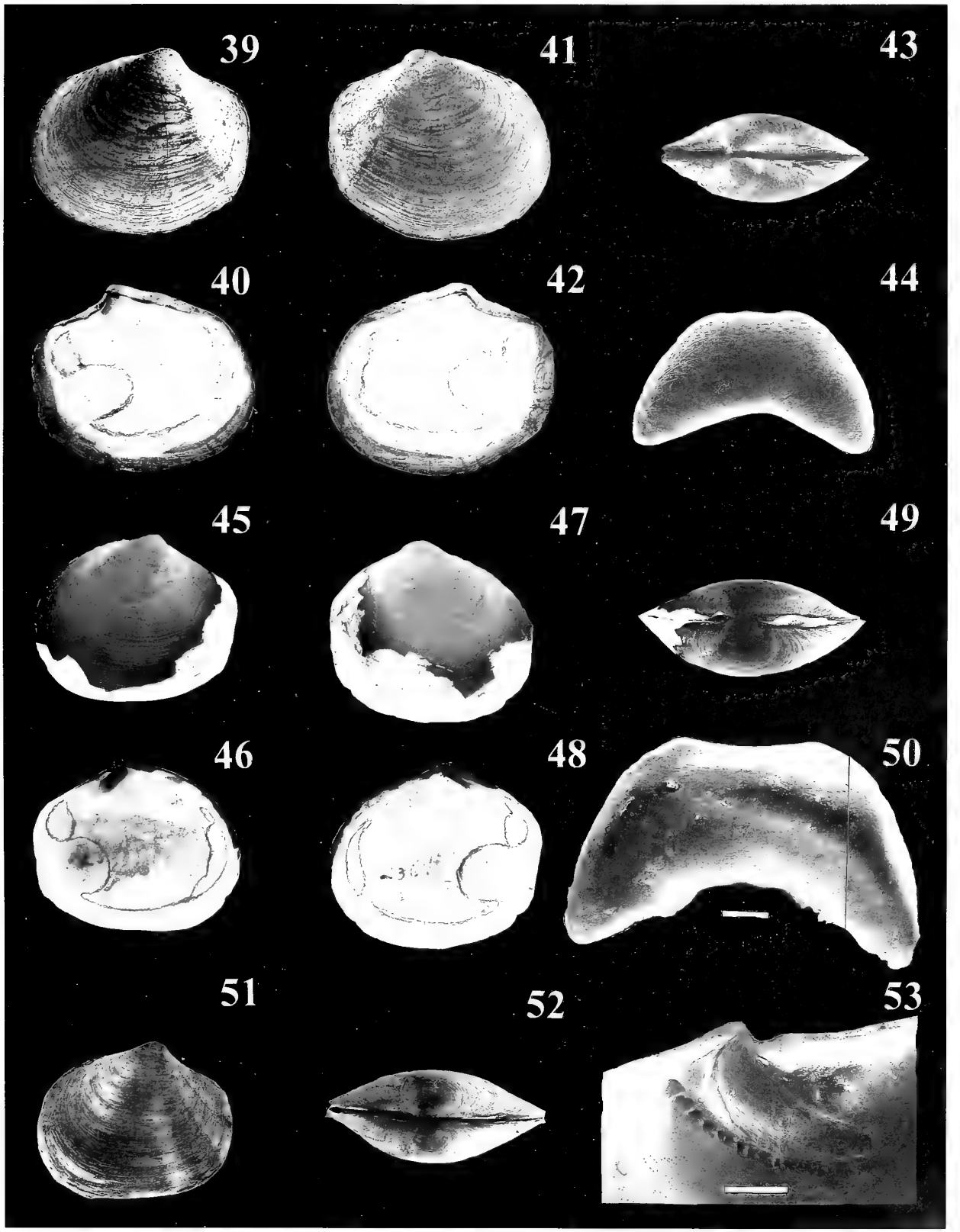
Explanation of Figures 39–53.

Lampeia adamsi (MacGinitie, 1959). Figures 39–44. Young specimen (MIMB 1/35177), Sakhalinsky Bay, Sea of Okhotsk (54°27′2″N, 141°50′8″E), 65 m depth. Figures 39, 40. Left valve, length 16.3 mm. Figures 41, 42. Right valve, length 16.6 mm. Figure 43. Dorsal view of both valves. Figure 44. Ventral view of lithodesma. Scale = 1 mm. Figures 45–53. Adult and young specimens (UAM 4473), Mys Chaplino, Chukotskiy Poluostrov, NW Bering Sea (64°18′50″N, 171°8′W), depth 41 m. Figures 45, 46. Left valve of an adult specimen, length 29.1 mm. Figures 47, 48. Right valve of an adult specimen, length 29.7 mm. Figure 49. Dorsal view of both valves of an adult specimen. Figure 50. Ventral view of lithodesma of an adult specimen. Scale = 1 mm. Figure 51. Left valve of a young specimen, length 15.4 mm. Figure 52. Dorsal view of both valves of a young specimen. Figure 53. Close-up of a right valve of a young specimen showing the buttressed subumbonal structure without ligament and the inner part of the dorsal margin near beak. Scale = 1 mm.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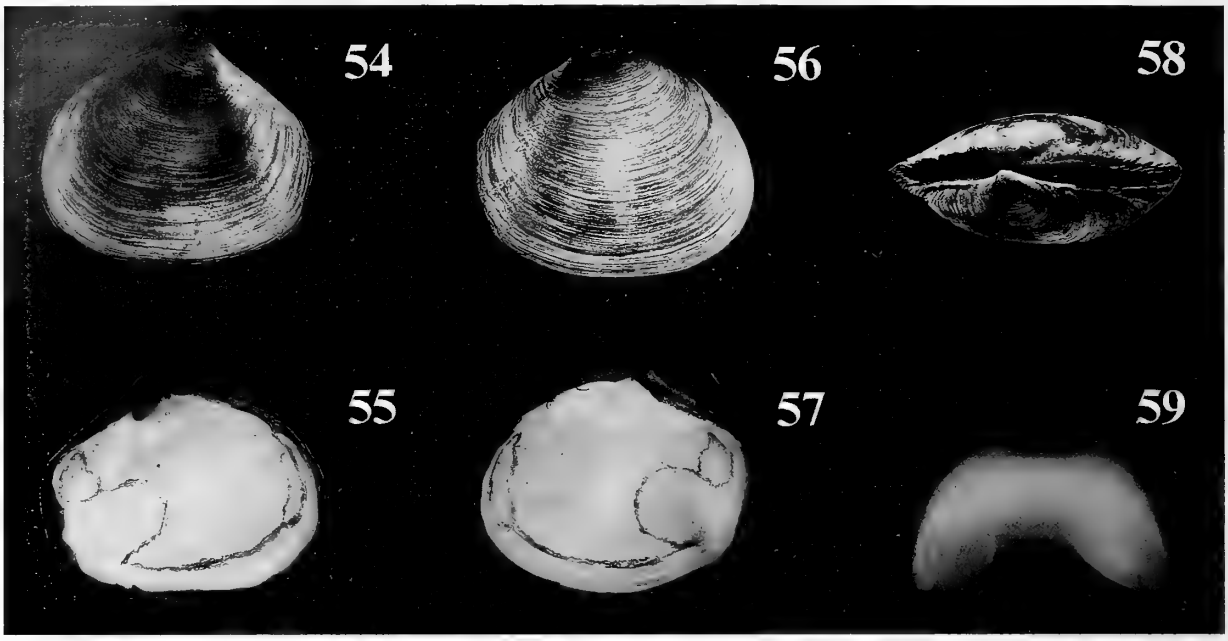

Explanation of Figures 54–59

Lampeia adamsi (MacGinitie, 1959). Adult specimen (MIMB 2/35178), west coast of Kamchatka, Sea of Okhotsk (54°N, 155°06′E), 85 m depth. Figures 54, 55. Left valve, length 25.2 mm. Figures 56, 57. Right valve, length 26.7 mm. Figure 58. Dorsal view of both valves. Figure 59. Ventral view of lithodesma, length 7 mm.

Lampeia adamsi (MacGinitie, 1959), Baxter, 1987:32; Coan, 1990:43–45, figs. 43, 43a, 44; Foster, 1991:133; Feder et al., 1994a:161.

Diagnosis: Shell ovately subquadrate; beaks slightly posterior to midlines, rounded, opisthogyrate; anterior end obtusely rounded; posterior end broadly subtruncate; anterodorsal margin convex; posterodorsal margin straight; posterior margin anteriorly directed; toothlike process on inner part of anterodorsal margin absent in right valve; pillars supporting subumbonal structure for lithodesma short and thin, separated from anterodorsal shell margin by a large, deep pit; lithodesma simple, very curved.

Description (expanded from that of MacGinitie, 1959, and Coan, 1990): *Exterior.* Shell small (to 29.7 mm, UAM 4473, NW Bering Sea), ovately subquadrate, thick, strong, white under periostracum, inequivalve, right valve higher, longer, much more inflated than left valve; periostracum fairly thick, adherent, brown, extending into inner shell surface, in dry shells easily peeling off along ventral margin; surface with conspicuous growth lines, without pustules; beaks rounded, opisthogyrate, slightly posterior to midline; anterior end obtusely rounded; posterior end broadly subtruncate, with a faint radial ridge extending from posterior portion of beaks to transition of posterior margin to ventral margin, with a few microscopic spines along lower two-thirds and a suggestion of a second row of spines midway of area posterior to ridge; anterodorsal margin convex, rather steeply extending ventrally, smoothly transitioning to a rounded anterior margin; ventral margin slightly curved in right valve, straight in left valve; posterodorsal margin straight, rather steeply extending ventrally, forming a smooth angle at transition to posterior margin; posterior margin straight, anteriorly directed, forming a very smooth angle at transition to ventral margin; lunule present only in left valve, wide, deep, well expressed along entire posterodorsal margin, demarcated by a ridge extending along anterodorsal margin from beaks to anterior margin; escutcheon wide, deep, more expressed in left valve, demarcated by ridges, extending along posterodorsal margin from beaks to dorsal margin.

Interior. Toothlike process on inner part of anterodorsal margin absent in right valve; elongate-trigonal subumbonal structure for lithodesma rather elongate; pillars thin, short, becoming thinner ventrally, their width equal to or less than the pits between them, separated from anterodorsal shell margin by a large, deep pit; number of pillars varies from 10 to 21; lithodesma large, very curved; interior of shell chalky; anterior adductor muscle large, elongate; posterior adductor scar large, rounded; pallial sinus short, broadly U-shaped in left valve, rounded, somewhat larger in right valve, stopping just short of midline; ventral edge of pallial sinus not confluent with pallial line.

Variability: Shell shape and proportions distinctly change with age (Table 4). In young specimens, in con-

trast to adults, the shell is much thinner, much more elongate, the shape closer to quadrangular; valves are less inflated; beaks sharper and placed more posteriorly; periostracum is lighter in color, yellowish-brown; in the posterior part of the shell the second row of spines can be more conspicuous or absent; anterodorsal margin straight and from the beaks extending almost horizontally, parallel to ventral margin; posterodorsal margin very smoothly extending ventrally; posterior margin slightly curved, almost vertically extending ventrally only slightly turned anteriorly; lunule in left valve absent; escutcheon shorter, narrower, much more weakly expressed. The number of the pillars varies and probably increases with shell size; some of the pillars may not be attached to shell wall.

Type material and locality: Holotype (USNM 610301), 4 km off Point Barrow, Arctic coast of Alaska (about 71°31′N, 156°23′W), 33.5 m depth, mud-gravel-stone bottom, Coll. G.E. MacGinitie, 15 September 1948 (MacGinitie, 1959; Coan, 1990).

Material examined: 1 lot (UAM 4473) from NW Bering Sea, Mys Chaplino, Chukotskiy Poluostrov (64°18′50″N, 171°8′W) (Coan (1990) made a minor mistake, giving the coordinates 64°18′30″N), depth 41 m, Coll. S. Stoker, 28 July 1973 (2 specimens and 2 right valves); 1 lot (MIMB 2/35177) from west coast of Kamchatka, Sea of Okhotsk (54°N, 155°06′E) (Figure 1), 85 m depth, sand + gravel + silt, bottom temperature +0.4°C, Coll. V.A. Nadtochy, 21 July 1996 (R/V *Professor Levanidov*) (1 specimen); 1 lot (MIMB 1/35177) from Sakhalinsky Bay, Sea of Okhotsk (54°27′2″N, 141°50′8″E), 65 m depth, large-particle sand, bottom temperature +1.5°C, Coll. V.N. Koblikov, 30 July 1977 (R/V *8-452*) (1 specimen).

Distribution and habitat: On the Arctic coast of Alaska, from off Point Barrow (71°34′N, 156°22′W) westward into the NW Bering Sea off Mys Chaplino, Chukotskiy Poluostrov (64°18′50″N, 171°8′W) (UAM 4473), 10–41 m (Coan, 1990); west coast coast of Kamchatka, Sea of Okhotsk (54°N, 155°06′E); Sakhalinsky Bay, Sea of Okhotsk (54°27′2″N, 141°50′8″E). In the Chukchi Sea on the Arctic coast of Alaska, between Point Barrow and Icy Cape (depth 23–30 m) this species was recorded on sand (97.6%) and sand (82.9–84.2%) + mud + silt at a bottom water temperature of 1–2°C (Feder et al., 1994a, b; H. M. Feder, personal communication). Off Point Barrow this species (type specimen) was recorded on mud-gravel-stone bottom (MacGinitie, 1959). In the Sea of Okhotsk (depth 65–85 m), this species was recorded on sand and sand + gravel + silt at a bottom water temperature of 0.4–1.5°C.

Comparison: This species is easily distinguished from *L. **triangula*** and *L. **posteroresecta*** by its ovately-subquadrate shell, lack of a toothlike process on the anterodorsal margin of the right valve, presence of a large, deep pit separating pillars of the subumbonial structure from the anterodorsal shell margin, and its simple, curved lithodesma.

DISCUSSION

Distribution

The species of *Lampeia* are clearly rare and occur only in small areas of the northwestern Pacific and Arctic. The eastern border of the habitat of the most studied species, *L. adamsi,* in the Arctic is Point Barrow, at the boundary between the Chukchi and Beaufort seas (156°) (Ushakov, 1952). This species was not found in the western part of the Beaufort Sea (Bernard, 1979). It is recorded only in the western part of the Chukchi Sea, where it is very rare. Thus, as a result of a detailed study of the composition and distribution of macrobenthos in the northeastern Chukchi Sea, *L. adamsi* was found only in a small area between Point Barrow and Icy Cape at three stations (CH 6, CH 17, CH 19) in seven samples (11 specimens) (Feder et al., 1994a, b; H.M. Feder, personal communication). In the northwestern part of the Bering Sea, this species was found also in the local area in two samples (UAM 4473 and 64°23′N, 169°31′W, 39.8 m) (N. R. Foster, personal communication). In the Sea of Okhotsk, we found it only in two samples. This species is thus very rarely represented in collections. Coan (1990), when studying the available material of thraciids in museum and private collections, found *L. adamsi* only in eight lots, including the type. The same thing can be said about the distribution of other species of this genus.

We have studied the materials of 15 expeditions of different institutes of Russia, which collected the samples of macrobenthos in the shelf zone of the western part of the Bering Sea and the southeastern Kamchatka from Bering Strait to Lopatka Cape (Kamchatka), the Commander Islands, all the Sea of Okhotsk and also the shelf and bathyal zones of all the Kurile Islands. In total, 1930 benthos stations were examined (4409 samples). *Lampeia* was found only at 10 stations. It is interesting that at the coastal zone of the western Kamchatka three PRIFO expeditions worked (R/V *Ekvator,* 1982; R/V *Dalny,* 1989; R/V *Professor Levanidov,* 1996), and collected benthos samples using a standard technique at the same stations. However, *L. **triangula*** was found in that region only in 1989 and *L. adamsi* only in 1996.

Lampeia, as compared with most representatives of the family Thraciidae, has a thick shell, which is very rarely damaged during the collection and treatment of benthos samples. Thus, the fact that only a few individual specimens were found in different parts of the northwestern Pacific Ocean and the Chukchi Sea is probably due only to their local distribution within their habitat area where they occur only at a low density. Thus, the average density of *L. adamsi* in the northeastern part of the Chukchi Sea at three stations varied from 6–8 ind/m^2 (H. M. Feder, personal communication) and in the Sea of Okhotsk was

4 ind/m^2. The population density of *L. **triangula*** near the western coast of Kamchatka, according to the results of two quantitative samples, was 4 and 8 ind/m^2. The population density of *L. **posteroresecta*** in the Fourth Kurile Strait was 8 ind/m^2.

Of the three species, *L. adamsi* is the more shallow-water species. In all parts of the species range, this species occurs at relatively shallow depths (10–85 m), mainly on sand or sand with a slight admixture of silt. The other two species were found at significantly greater depths (*L. **triangula,*** 144–214 m, *L. **posteroresecta,*** 180–500 m) and only on silty sand or sandy silt. Probably, the great differences in habitats account for the marked morphological differences between *L. adamsi* and the more closely related *L. **triangula*** and *L. **posteroresecta.***

Inner Shell Morphology

It is known that representatives of the family Thraciidae have a edentulous hinge. Only the juveniles of *Thracia curta* have an anterior lateral tooth in the right valve, and it disappears with growth (Coan, 1990). As we already mentioned, *L. **triangula*** and *L. **posteroresecta*** have a conspicuous toothlike process on the anterodorsal shell margin of the right valve; it is very similar in its shape and structure to a true lateral tooth. However, despite this similarity, it cannot be considered a true tooth for a number of reasons. In the left valve of both species, there is no tooth or cavity on the inner part of the dorsal margin that would correspond to this process. The inner part of the dorsal margin in the left valve is straight and smooth, and is only slightly concave just anterior to the beak to match the toothlike process in the right valve when the valves are closed. In almost all the *L. **triangula*** studied, with the exception of a few juvenile specimens, the toothlike process is completely covered with periostracum. It is evident that it does not extend into the inner part of the shell. The lower part of this process fits into a small depression in the lithodesma and probably provides a better attachment of the lithodesma to the shell. Because of the small depression for the toothlike process on one side, the lithodesma, despite its variability, has a butterflylike shape only in *L. **triangula*** and *L. **posteroresecta.***

In the studied specimens of *L. **posteroresecta,*** the toothlike process is more conspicuous and is not covered with periostracum. However, it may also be covered with periostracum, which was damaged and fell away in the process of opening the shell. In all the specimens of this species, in the area of the toothlike process, we found fresh fractures on the periostracum. Probably, the periostracum broke away because, in contrast to *L. **triangula,*** the material of this species was stored dry and the periostracum became more fragile.

The subumbonal structure for the lithodesma of *Lampeia* is also of considerable interest. As Coan (1990) said, the buttressed subumbonal structure is unique. MacGinitie (1959), in describing *L. adamsi,* gave an exact number of the pillars supporting this structure. Our studies of the two new species, show that the exact number of the pillars is very difficult to determine because some of them either bifurcate ventrally or are not connected to the shell wall and look like stalactites. Moreover, the number of pillars within each of the species can vary rather greatly. Thus, the number of pillars is probably not a reliable character in identifying species of *Lampeia.* In this case, we can only say that some species have more pillars than others. On the other hand, the shape of the pillars does not vary much within a species, and this characteristic may be much more species-specific.

In general, the number of the pillars was equal in both valves. However, because it is sometimes very difficult to count the number of pillars, we may have made errors in calculations. Thus, in the future, when more studies will be made using additional material, it is possible that the number of pillars in different valves of some specimens will be found to differ.

Note Added in Proof: While the present paper was in press, Mr. A Yu. Voronkov (Zoological Institute, St. Petersburg) informed us about the first record of *Lampeia adamsi* from the western Chukchi Sea (68°38′1″N, 177°58′8″E), 33 m depth, sandy site, coll. B. J. Sirenko, 27 August 1989 (R/V *Dmitry Laptev*).

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THE VELIGER

Functional Anatomy of *Nausitora fusticula* (Jeffreys, 1860) (Bivalvia: Teredinidae)

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Abstract. A study of the functional anatomy of *Nausitora fusticula* (Jeffreys, 1860) correlated with the habitat of the species was made. Special attention was paid to the siphons, pallets, and musculature associated with them, ctenidia, labial palps, foot, and mantle. The analysis of the siphons revealed the presence of cilia, not described for any Teredinidae previously studied. Each ctenidium of *N. fusticula* is formed only by the external demibranch, with the blades in a "V" form. The ctenidia, associated with the rejection tracts of the mantle, present a good mechanism to deal with large quantities of particles, possibly an adaptation for life in turbid waters. The labial palps are extremely reduced. Analysis of the foot ciliary currents revealed that the foot participates in the removal of wood fragments produced by the action of the shell against the gallery wall, and that only part of these fragments are ingested, the remainder being eliminated as pseudofeces. The functional anatomy of *N. fusticula* suggests that for this species plankton probably is a more important food item than wood.

INTRODUCTION

The anatomy of species of Teredinidae has been studied by several authors, including Quatrefages (1849), Menegaux (1889), Ridewood (1903), Sigerfoos (1908), Potts (1923), Lazier (1924), Atkins (1937), Purchon (1939, 1941, 1960), Turner (1966), Rancurel (1971), and Saraswathy & Nair (1971).

Little is known about the functional anatomy of the Teredinidae. The only references on the subject are the studies of Atkins (1937), Purchon (1941, 1960), Morton (1970, 1978), and Martinez (1987), which focus mainly on the structure and function of certain specific organs.

The functional anatomy of *Nausitora fusticula* (Jeffreys, 1860) is the main focus of this work; we analyze the functioning of the siphons, the muscles associated with siphons and pallets, and the ciliary currents related to the selective mechanism of food capture and particle elimination. A detailed study of the anatomy and function of the stomach is presented in a separate paper (Lopes et al., in press).

Nausitora fusticula occurs in the West Atlantic tropical region (Turner, 1971). On the Brazilian coast it occurs only in mangroves and has been reported from the littoral of São Paulo State (Bartsch, 1922; Turner, 1966; Lopes & Narchi, 1993); and of Paraná State (Muller & Lana, 1986, 1987).

This is the first study made on the functional anatomy of a species of the genus *Nausitora* Wright, 1864, which includes six species (Hoagland & Turner, 1981). Among them, Turner (1966) described the anatomy of *N. dunlopei* Wright, 1864, and Saraswathy & Nair (1971) the anatomy of *N. hedleyi* Schepman, 1919.

MATERIALS AND METHODS

Specimens were collected in mangrove trees at Praia Dura, Ubatuba, São Paulo, Brazil (45°15′W, 23°30′S). This is the most abundant species of Teredinidae in the area, living in a salinity range from 0–33 S (Lopes & Narchi, 1993). The animals were kept inside the wood, in a seawater aquarium with constant aeration and a salinity of 20 S at a room temperature of 22°C, where they stayed in good conditions for over 6 months.

Living and preserved specimens, totaling around 100 specimens of all sizes, were analyzed. Identification of the material was based on Turner (1966, 1971). A lot of 20 complete specimens (shell, pallets, and soft parts) was deposited at the Museu de Zoologia, Universidade de São Paulo (MZUSP) under the registration number 28598.

Ciliary currents were studied by the application of suspensions prepared with Carborundum grade F3, carmine, and Aquadac powders.

Some of the anatomical details analyzed were obtained by transverse sections (6–8 μm thick) of animals fixed in Bouin's fluid and stained with Mallory's Triple Stain or Ehrlichs's hematoxylin and eosin, according to the methods described by Pantin (1948).

RESULTS

General Disposition of Organs in the Mantle Cavity

The disposition of the major organs in the mantle cavity of *N. fusticula* is shown in Figure 1.

When the gonads are fully developed, the visceral mass

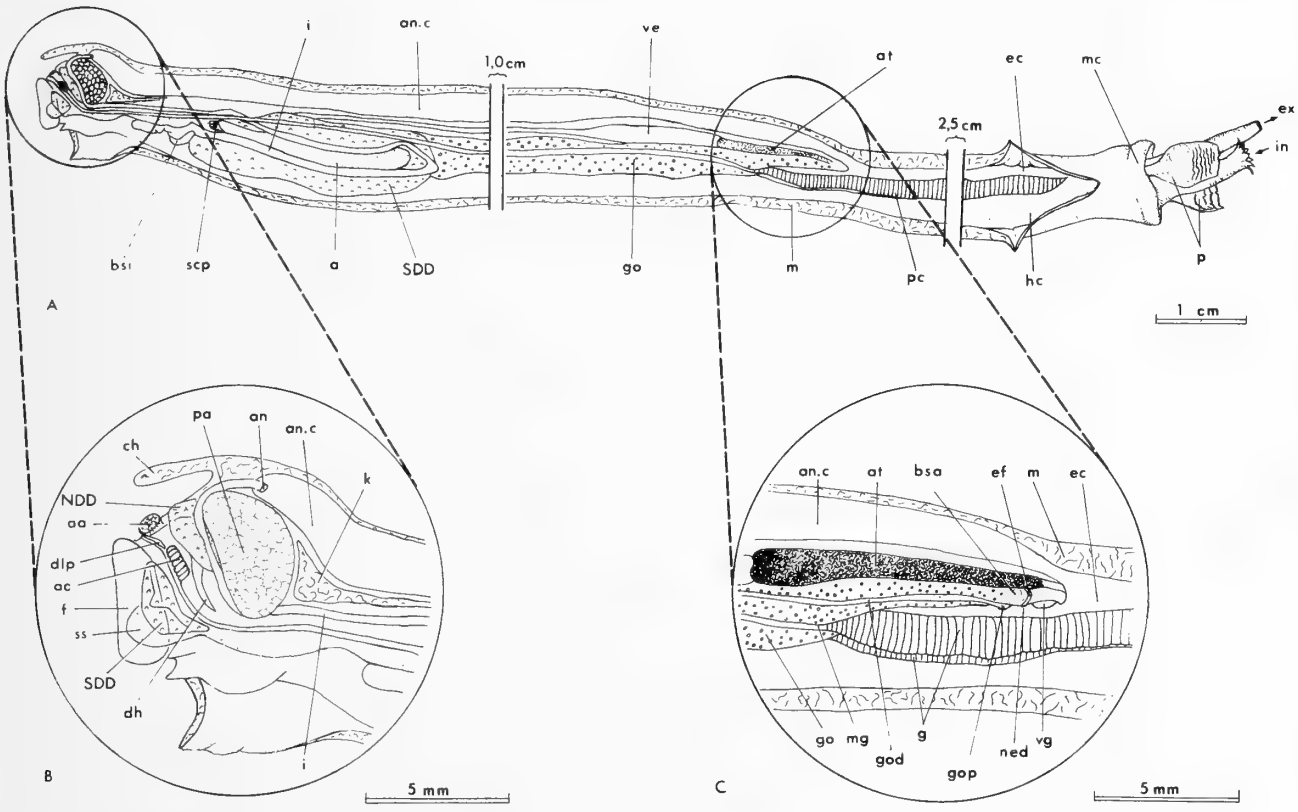


Figure 1

Nausitora fusticula. A. General topography of the organs after removal of the valve and the mantle from the left side of the body. B. Details of the anterior region. C. Details of the gonopore and nephridiopore regions after slight displacement of the ctenidia to expose the epibranchial cavity underneath the distal extremities of the gonads. **a,** appendix; **aa,** anterior adductor muscle; **ac,** anterior ctenidium; **an,** anus; **an.c,** anal canal; **at,** atrium; **bsa,** bulblike swelling of the afferent excretor duct; **bsi,** bulblike swelling of the intestine; **ch,** cephalic hood; **SDD** and **NDD,** respectively, specialized and normal digestive diverticules; **dh,** dorsal hood; **dlp,** dorsal labial palp; **ec,** epibranchial cavity; **ef,** efferent excretor duct; **ex,** exhalant siphon; **f,** foot; **go,** gonad; **god,** gonoduct; **gop,** gonopore; **hc,** hypobranchial cavity; **i,** intestine; **in,** inhalant siphon; **k,** main portion of the kidney; **m,** mantle; **mg,** marginal groove; **mc,** mantle collar; **ned,** nephridiopore; **p,** pallet; **pa,** posterior adductor muscle; **pc,** posterior ctenidia; **ss,** crystalline style sac; **ve,** ventricle; **vg,** visceral ganglion.

occupies about 60–70% of the body length and the posterior ctenidia occupy the remainder.

The stomach is long; the appendix or wood-storing caecum in the live animal is easily distinguished from the other structures because of the reddish color caused by the particles inside it. The appendix is about 14–20% of the body length.

The digestive diverticula (Figure 2) are of two types as defined by Potts (1923) and Morton (1970) for *Teredo navalis* Linnaeus, 1758: the normal type (NDD) and the specialized type (SDD). In live specimens of *N. fusticula,* the former has a dark brown coloration and the latter a light pink color.

Males or females have milky white gonads, situated at the region immediately posterior to the distal part of the digestive diverticula. In animals with undeveloped gonads, the anterior part of the posterior ctenidium extends over the appendix. Upon maturation, the gonads develop and occupy the space between the appendix and the posterior ctenidia, pushing the posterior ctenidium to the rear part of the body.

In animals measuring up to 4.5 cm in length we found specimens of the same size with differing degrees of gonadal development. In animals over 4.5 cm in length, the only variations observed pertained to the increase in gonad size, and, in some animals, to the spreading of the gonads over the posterior third of the appendix.

The heart of *N. fusticula* shows two atria with a very dark brown color due to the great abundance of reno-pericardial glands over the external wall. The ventricle has a whitish color and from it arises the well-developed aorta, which is located on the dorsal surface of the gonads.

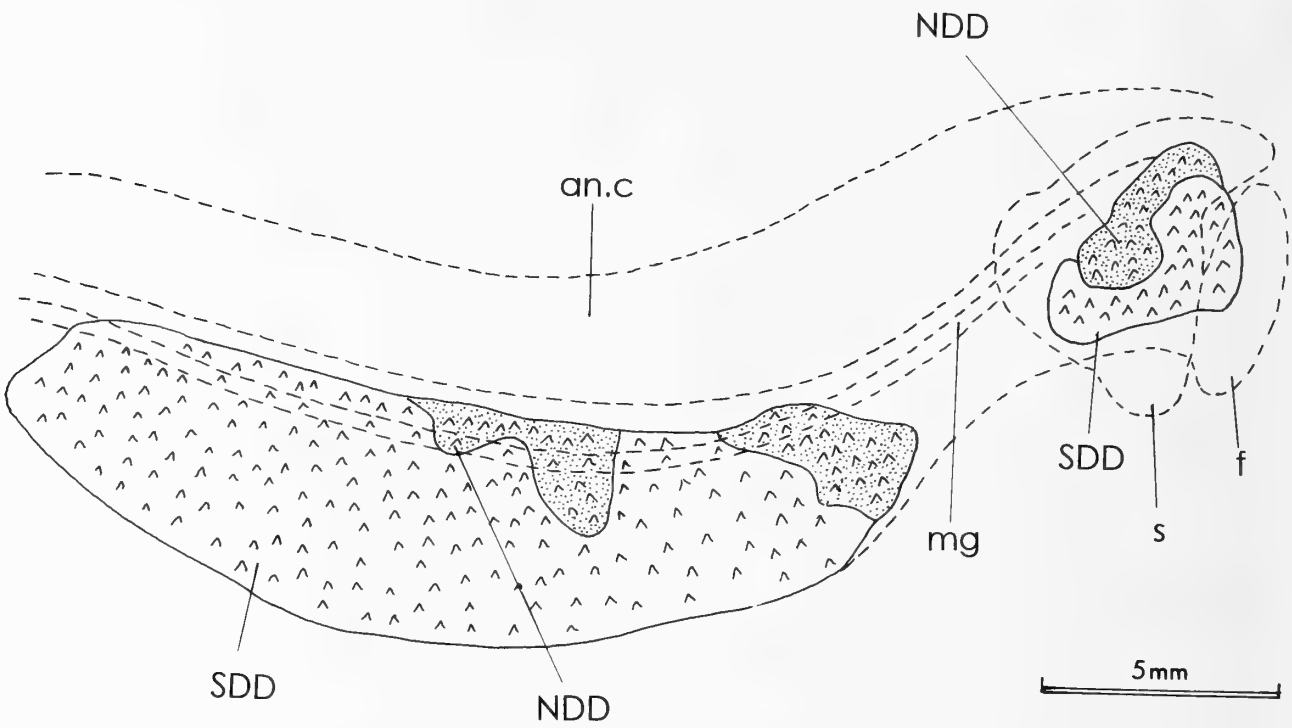


Figure 2

Nausitora fusticula. Disposition of the specialized (**SDD**) and normal (**NDD**) digestive diverticula when the animal is observed from the right side. **an.c,** anal canal; **f,** foot; **mg,** marginal groove; **s,** shell.

The kidneys are dorsal to the aorta, extending from the posterior part of the posterior adductor muscle to the distal extremity of the pericardial cavity. The nephrostoma opens into the interior of the pericardial cavity and the nephridiopores into the epibranchial cavity, both at the same level of the body (Figure 3A). The excretor afferent duct shows, just after the nephrostoma, a globular dilatation with the internal wall deeply folded and ciliated (Figures 3A, 4). The two nephridiopores are placed near to each other, being much smaller than, and situated posteriorly to, the gonopores (Figure 3A). Each of the gonopores possesses two dilatations: one larger and the other smaller, anteriorly and posteriorly located, respectively (Figure 3A).

The anal canal occurs in the dorsal region of the visceral mass and extends from the anus to the posterior end of the gonads, connecting to the epibranchial cavity through a narrow opening (Figures 1, 3B).

Shell

The nomenclature used in the description of the shell is that adopted by Turner (1966). Less than half of the external surface of the shell of *N. fusticula* (Figure 5A) is occupied by the anterior slope. The dorsal region possesses denticulated ridges that are eroded by friction against wood; at the lateral region these ridges are more evident. The umbonal-ventral sulcus is narrow and flat. The dorsal and ventral condyles are well developed, but the umbonal-ventral ridge is poorly defined. The apophysis is flat when viewed transversely, with a sharp extremity near the ventral condyle. The adductor posterior muscle scar is weakly evident (Figure 5B).

Pallets

Each of the pallets of *N. fusticula* possesses a long stalk, of the same length as or longer than the blade. The blade is asymmetric in relation to the stalk axis, being 1.5–3 times longer than wide; its various cones, partially fused, are more evident when the pallets are observed from the inner face. The thick, brown periostracum covers each cone, forming long awns. At the distal region of the external face of the blade, the presence of a calcareous papillary encrustation is common; this encrustation may not appear in young specimens or in worn pallets. Among the specimens, the blade form varies (Figure 6). These variations could not be related to age or maturity of the animals, or to environmental conditions. All specimens analyzed came from the same population and similar ecological conditions. This can be interpreted only as individual variation.

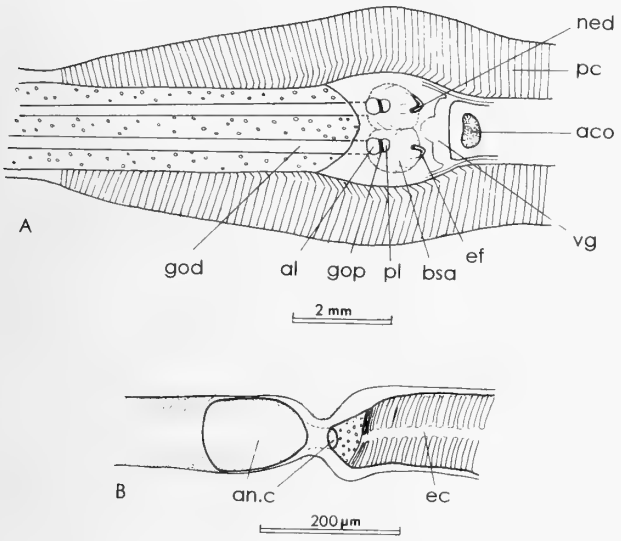


Figure 3

Nausitora fusticula. A. Roof of the epibranchial cavity after incision and separation of the two posterior ctenidia (**pc**), **aco,** anal canal opening; **al,** anterior lip of the gonopore; **bsa,** bulblike swelling of the afferent excretor duct; **ef,** efferent excretor duct; **god,** gonoduct; **gop,** gonopore; **ned,** nephridiopore; **pl,** posterior lip of the gonopore; **vg,** visceral ganglion. B. Detail of the anal canal (**an.c**), and its narrow opening in the epibranchial cavity (**ec**).

Siphons

The inhalant and exhalant siphons are joined for half of their length. Some specimens have siphons which are almost plain white in color, but most of them are white with small spots of reddish brown pigmentation from the separation of the siphons to their tips. This pigmentation is more abundant on the ventral side of the inhalant siphons and on the dorsal side of the exhalant siphons.

The inhalant siphon (Figures 7, 8) is fringed with a row of six large tentacles that are divided almost from their basal region, giving the appearance of 12 tentacles. When the animal is pumping water, the siphons project out of the opening and the tentacles remain almost perpendicular to the axis of the siphons.

Each tentacle has lobed lateral margins with high walls which form grooves that converge to a deep principal groove in the middle of the tentacle.

Around the opening of the inhalant siphon and at the base of the tentacles, there are alternately six well-developed and six smaller digitiform projections pointing toward the lumen of the siphon. Each is formed in the inner wall by a short fold which gradually ends as it becomes more internal. Thus the opening of the inhalant siphon presents six bifid tentacles directed to the outside and 12 digitiform projections (six large and six small) directed to the inside of the opening. The exhalant siphon possesses a relatively narrow opening, whereas the rim is smooth and lacks tentacles (Figure 7).

The exhalant siphon stretches and moves more actively than the inhalant one. The latter stayed in the same position for a long time, moving only when disturbed or in order to quickly close the opening by flexing the tentacles. This movement apparently occurred without any tactile stimulus and was not regular. When a suspension of carmine and Carborundum was added to the water near the inhalant siphon opening, the particles of carmine, as well as some small and medium-sized particles of Carborundum, were indiscriminately drained in the inhalant current and immediately rejected as pseudofeces. Larger particles which by chance fell into the center of the opening without touching the digitiform projections passed to the mantle cavity but were afterward rejected. Those that fell on the digitiform projections or on the tentacles were passively retained. No active movement of the structures of the inhalant opening was observed, in the sense of avoiding the entrance of large particles, or to eliminate those that settled thereon. However, when we added a large quantity of particles of carmine, and, especially Carborundum, to the surrounding water, the inhalant siphon reacted by contracting the circular muscle bundle near the base of the tentacles, thus closing the opening and drawing together the digitiform projections. This contraction always occurred in this place and was not accompanied by retractions of the tentacles, which remained partially extended. It was noted that some small particles of carmine, on entering into contact with the lobed edges of the inhalant siphon tentacles, were carried out by means of a weak rejecting current produced by cilia. Thus these cilia contribute to cleaning the tentacle surfaces, impeding the settling of small particles. At no time was filtration of suspended material by means of the inhalant tentacles observed. The presence of cilia on the siphons has not been described in any Teredinidae previously studied.

Nausitora fusticula eliminates feces and pseudofeces through small jets by means of the exhalant and inhalant siphons, respectively, throwing them a short distance away from the opening in the wood, where generally they accumulate. Fecal pellets are not formed. In the aquarium, large quantities of this waste accumulate, requiring weekly removal.

Musculature of the Pallets and Siphons

The musculature involved in moving the pallets (Figure 9) includes the protractors, anterior retractors, median retractors, posterior retractors, and adductor muscles. These muscles are peculiar to the Teredinidae, fixed to the proximal third part of the pallet stalk.

The protractor muscle of each pallet is composed of two well-developed muscular bundles, easily noted externally as an open fan shape, with the narrower part directed to the anterior region of the animal. The muscle

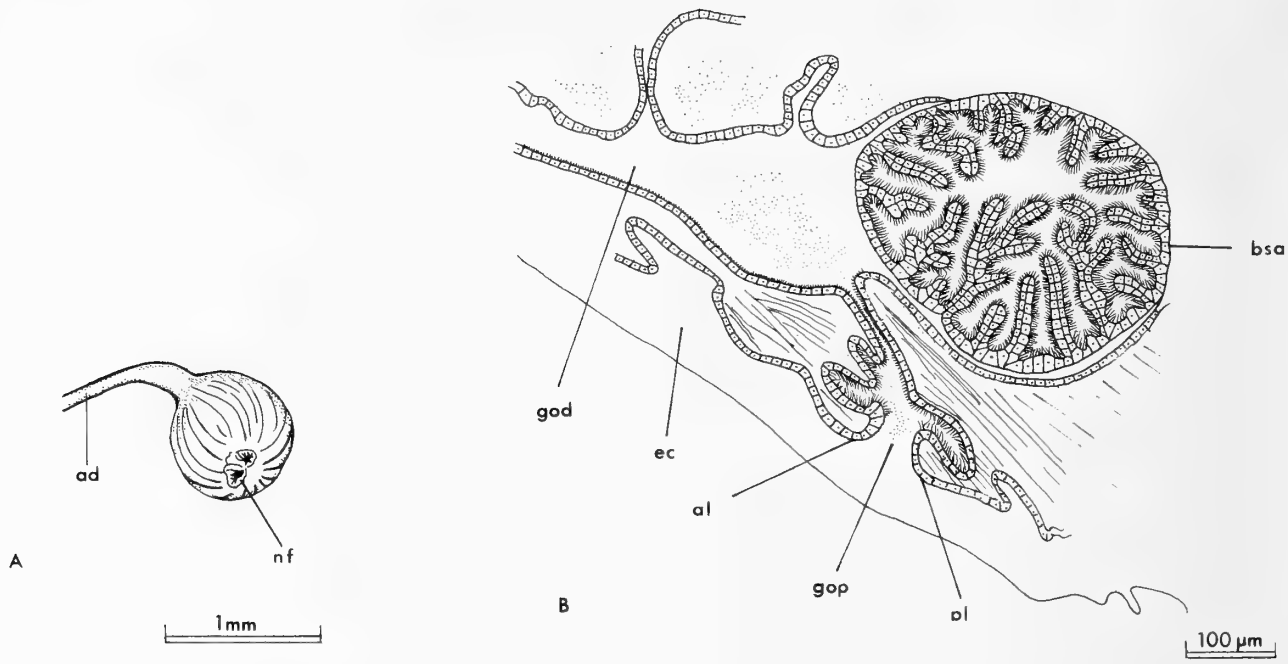


Figure 4

Nausitora fusticula. A. External view of the bulblike swelling of the afferent excretor duct (**ad**); **nf,** nefphrostome. B. Longitudinal section of the region of the body illustrated in "3A." **al,** anterior lip of the gonopore; **bsa,** bulblike swelling of the afferent excretor duct; **ec,** epibranchial cavity; **god,** gonoduct; **gop,** gonopore; **pl,** posterior lip of the gonopore.

itself is fixed to the stalk and to the calcareous part of the gallery wall.

The anterior retractor muscle of each pallet is formed by two muscular bundles, the thicker one herein designated "internal," and the other, thinner one designated "external." The internal bundle is fixed to the internal face of the stalk, extending toward the anterior region of the animal. It ends fixed to the calcareous coating of the gallery wall by an almost triangular area. In an animal removed from its gallery, this insertion area is externally visible near and ventral to the narrower region of the protractor muscle. The external bundle is fixed at the external face of the stalk, passes through the dorsal and ventral bundles of the protractor muscle of the pallet, and ends together with the internal bundle.

The median retractor muscle of the pallets is composed of only one bundle, fixed to the external face of the stalk. It passes between the dorsal and ventral bundles of the protractor muscle and ramifies at the same time that it extends laterally inside the mantle, ending near the midregion of the epibranchial cavity. At this point the muscle does not attach to any hard structure, but just ends inside the mantle.

The posterior retractor muscle is slim with little branching. It originates fixed at the free extremity of the pallet stalk and extends laterally inside the mantle to the region where the aorta begins. As is the case of the median retractor, the posterior retractor ends inside the mantle, not attached to any hard structure.

The two pallets are brought together by a narrow muscular bundle called the "adductor muscle of the pallets." Each of these muscle extremities is fixed to the internal face of the stalk at an area near to the insertion of the posterior retractor muscle.

In the body region where the musculature of the pallets occurs, it is possible to observe two well-developed cylindrical muscular bundles of the retractor muscles of the siphon. Each of these begins at the base of the siphons and is fixed to the gallery wall, together with the anterior retractor muscle of the pallet.

When the animal is pumping water, the pallets remain sheltered inside the gallery. Any disturbance in the environment causes retraction of the siphons. At this time, the pallets are pushed into the opening of the gallery by contraction of the pallet protractor muscles. Simultaneously, the two retractors and adductor muscles relax, causing contact of the pallet blades, thus forming a sort of stopper that closes the gallery entrance. When the disturbance ceases, the pallets retract, and the siphons stretch out to the exterior. Pallet retraction is executed by retractor muscles at the same time that the adductors contract, thus moving the pallet blades apart, allowing for passage

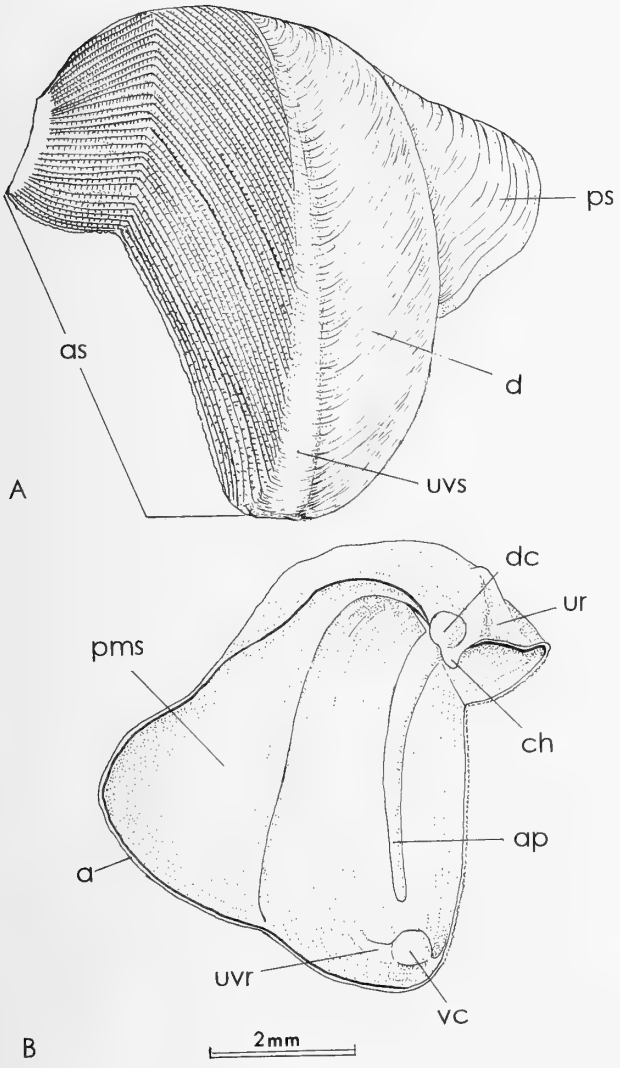


Figure 5

Nausitora fusticula. Left valve of the shell. A. External view. B. Internal view, **ap,** apophysis; **as,** anterior slope; **ch,** chondrophore; **d,** disc; **dc,** dorsal condyle; **ps,** posterior slope; **pms,** posterior adductor muscle scar; **ur,** umbonal region; **uvr,** umbonal-ventral ridge; **vc,** ventral condyle; **uvs,** umbonal- ventral sulcus.

of the siphons. During this process, the protractor muscles of the pallet and the retractors of the siphons remain relaxed.

Mantle

The mantle is very thin and transparent in the anterior third of the body of *N. fusticula.* At the median third, it is a little thicker laterally and ventrally, while at the posterior third, it is very thick. The tissue of the mantle is filled with a whitish substance, in which various groups of round granules of a reddish-brown color are immersed.

In the hypobranchial cavity, the internal epithelium of the mantle shows, at each side of the body, a tract with well-developed cilia, that extend from the anterior region to the base of the inhalant siphon. In the anterior and median regions of the body, these tracts are lateral, but at the beginning of the posterior ctenidia, they become ventral and approach one another without meeting.

In the dorsal part of the mantle, near the base of the exhalant siphon, there is a small glandular structure (Figure 10A, B), the special mantle gland.

The internal epithelium of the mantle in the epibranchial cavity dorsal to the posterior ctenidia is ciliated. Throughout the roof of this cavity, the tissue shows a thick zone of mucus cells. Histological sections of the dorsal mantle near the base of the exhalant siphon (Figure 10C) show the globular cells of the mucus zone and, dorsal to it, the flat acinus of the special gland of the mantle.

Ctenidia

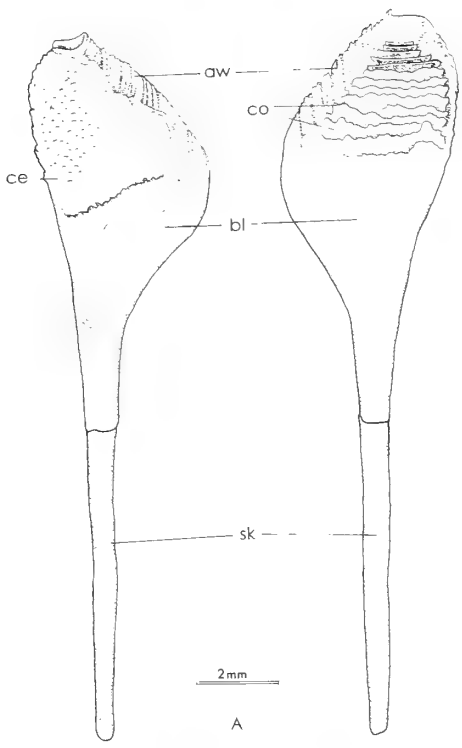
The nomenclature adopted in the description of the ctenidia of *N. fusticula* is the same used by Ridewood (1903), Atkins (1937), and Purchon (1939).

The posterior ctenidium of *N. fusticula* are completely unfolded. Depending on the condition of the body contraction, the ctenidium may become strongly folded, simulating a plait (Figures 1, 11A). The body of *N. fusticula* can be reduced to half of its length in preserved animals or even in live ones removed from wood. The posterior part of the body, where the posterior ctenidia are, is more affected by this contraction, and the ctenidia become shorter and folded.

For each of the posterior ctenidia there is only one demibranch, the external one, based on the disposition of the efferent and afferent vessel (Figure 11B), which is in accordance with Purchon (1939, 1941). The demibranch connects loosely to the wall of the mantle. Internally and dorsally to this area of union, the efferent branchial vessel occurs (Figure 11B, C), conducting oxygenated blood from the ctenidium to the atria. The axis of the right demibranch is fused to the axis of the left demibranch throughout the median line of the body. The afferent branchial vessel is situated dorsally and internally to the line of fusion.

The demibranchs of *N. fusticula* are characterized as eulamellibranch and homorrhabdic. Each demibranch has a V-shaped form in which the apex possesses a marginal groove 58–69 μm deep. When the demibranch is in a relaxed condition, the "V" apex is turned to the ventral-lateral region of the animal (Figure 11B). When contracted, it may be directed to the lateral part of the animal, giving the impression that the demibranch is broad and flat; the third dorsal part of the external lamella filaments becomes almost horizontal, resembling the vestige of another demibranch (Figure 11C).

At each side of the internal wall of the afferent bran-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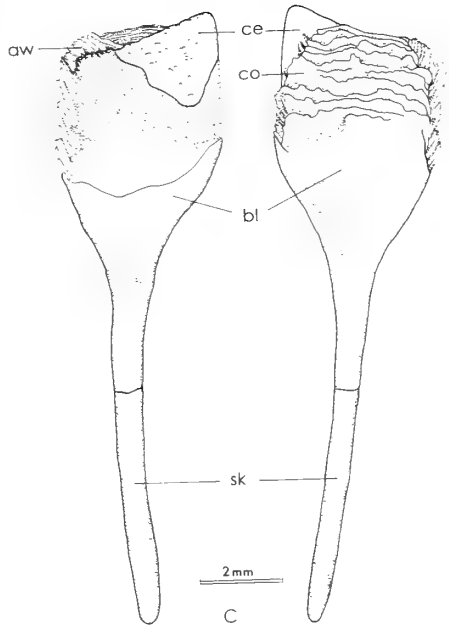
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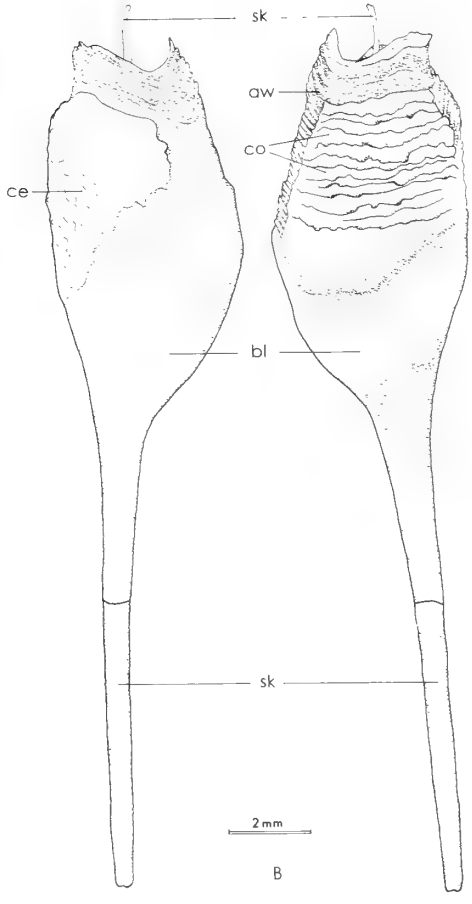
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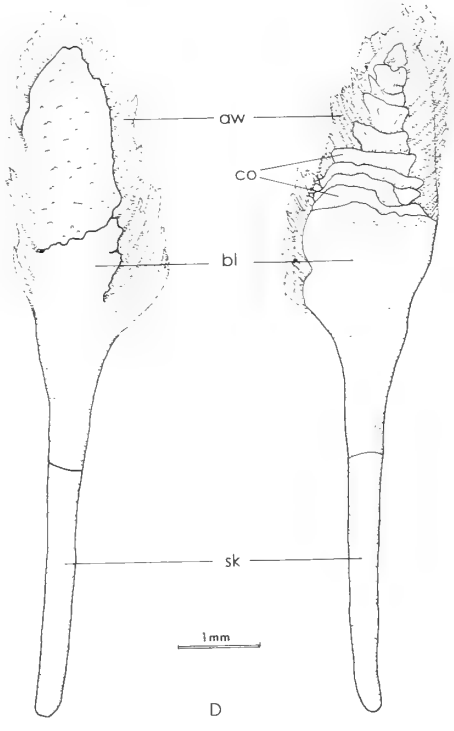
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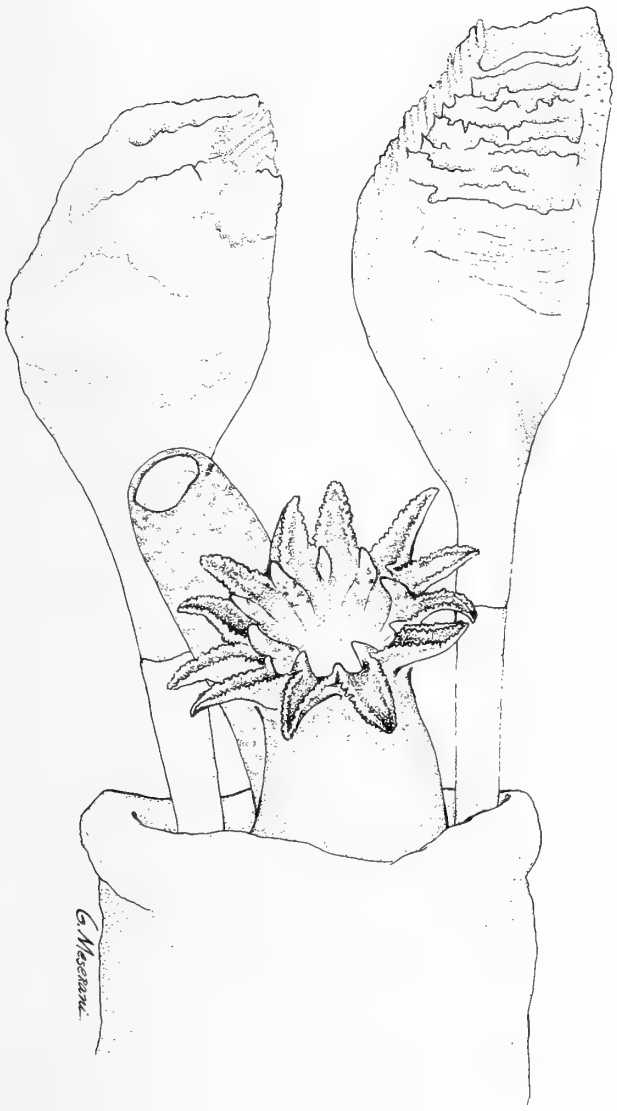

Figure 7

Nausitora fusticula. Siphons and pallets as observed in living animal removed from the wood.

chial vessel there is a duct of the Deshayes glands (Figure 11B, C). Analysis of histological sections of *N. fusticula* shows the extent of these ducts to the beginning of the anterior ctenidia.

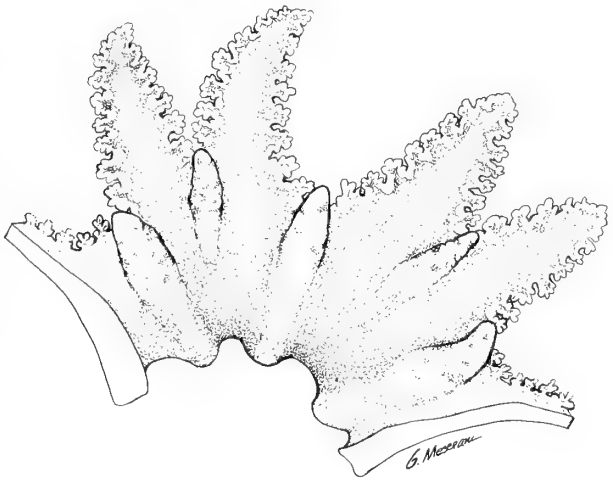

Figure 8

Nausitora fusticula. Detail of the inhalant siphon showing two bifid tentacles with deeply cut and lobed edges.

Each filament of the posterior ctenidia measures around 37 μm in width along practically its entire length, with the exception of the free extremity, which is slightly dilated. Each filament (Figure 12) presents a fore-strip of frontal cilia (fc), each of which measures around 8.3 μm in length, bordered by two rows of lateral-frontal cilia of about 13.4 μm in length; laterally, between the base of the filament and the lateral-frontal cilia, there are lateral cilia (lc) of around 10.0 μm in length forming on each face a strip of about 18.0 μm in width. Between the lateral-frontal and frontal cilia there is a strip without cilia. The frontal cilia cover the free extremity of filaments, always showing the same length. In this region there are no larger cilia which could be identified as being terminal. The rows of lateral-frontal and frontal cilia curve slightly in the direction of the marginal groove base, where they end. The cilia localized on the marginal groove are practically of the same length as the frontal cilia.

The posterior demibranchs of *N. fusticula,* joined by their respective ctenidial axis, are separated at the posterior region of the visceral mass. Simultaneously, the filaments become smaller in size until they are reduced to the marginal groove. This groove is laterally situated on the visceral mass, extending to the anterior ctenidia, and is bordered by prismatic ciliated cells.

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Figure 6

Nausitora fusticula. Variations in the pallet form. Each pallet is represented by its external and internal view. A, B, C, D, pallets from different specimens of the same population. **aw,** awns; **bl,** blade; **ce,** calcareous encrustation; **co,** calcareous cone; **sk,** stalk.

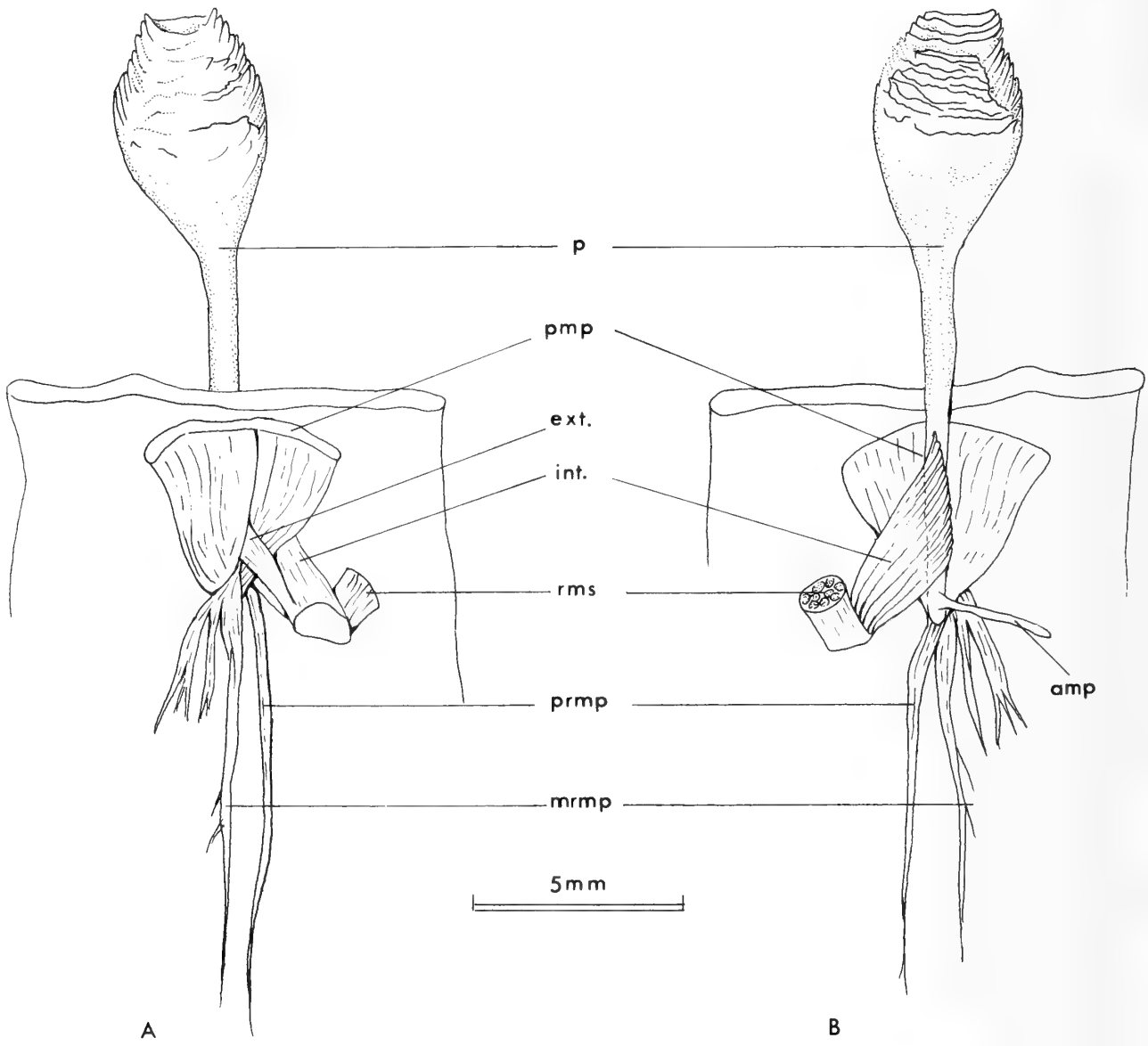

Figure 9

Nausitora fusticula. A. External view. B. Internal view, of the muscles associated to the pallets and siphons; **amp,** adductor muscle of the pallet; **int.** and **ext.,** respectively, internal and external bundles of the anterior retractor muscles of the pallet (**armp**); **mrmp,** mid-retractor muscle of the pallet; **p,** pallet; **pmp,** protractor muscles of the pallet; **prmp,** posterior retractor muscle of the pallet; **rms,** retractor muscle of the siphon.

The anterior ctenidium has from six to eight filaments that correspond to those of the external lamella of the demibranch (Figure 13). Each filament is reduced to a simple bar, joined throughout all of its length to the epithelium of the visceral mass. The first and last filaments really are semi-filaments because there is complete ciliation on only one of the lateral faces.

Labial Palps

The labial palps of *N. fusticula* (Figure 13) are attached to the epithelium of the visceral mass, which is the most common form among the Teredinidae. They are almost inconspicuous, the external one occupying a dorsal position, and the internal one, a ventral position. The dorsal palp is reduced to a narrow, flat fold, except for a slight

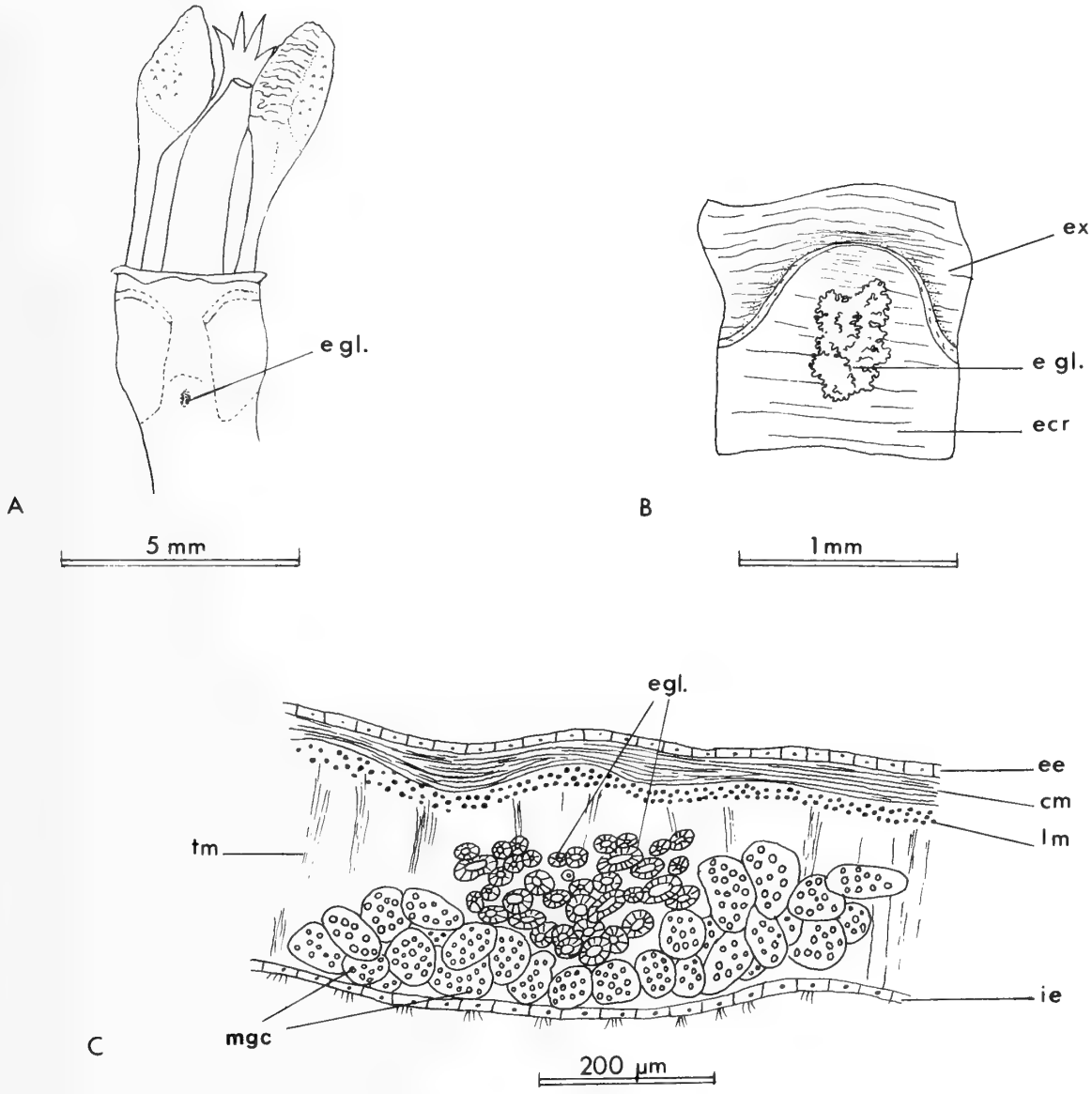

Figure 10

Nausitora fusticula. A. Dorsal view of the posterior extremity to show the localization of the special mantle gland (**e gl**). B. Internal view, epibranchial cavity roof, near to the exhalant siphon base showing the general appearance of the special mantle gland as seen in specimens where the gland is well developed. **ecr,** epibranchial cavity roof; **e gl,** (as in A); **ex,** basal wall of the exhalant siphon after removal. C. Histological transverse section of the special gland of the mantle. Note the presence of mucus gland cells (**mgc**) together with the acinus of the special gland of the mantle (**e gl**); **cm,** circular muscle bundle of the mantle; **ee,** external epithelium of the mantle; **ie,** internal epithelium of the mantle in the epibranchial cavity; **lm,** longitudinal muscle bundle of the mantle; **tm,** transversal muscle bundle of the mantle.

corrugation on the dorsal face. Each fold is placed between the mouth and the anterior ctenidia. The ventral palp is vestigial, being reduced to a small, long, and narrow elevation extending from the ventral border of the mouth to the anterior extremity of the marginal groove. Identification of the palp was possible only for some specimens, since the appearance of wrinkles is common around the mouth, making it difficult to distinguish the ventral palp.

Ciliary Currents

On the filament of the internal and external blades of each demibranch, the lateral cilia wave, causing strong

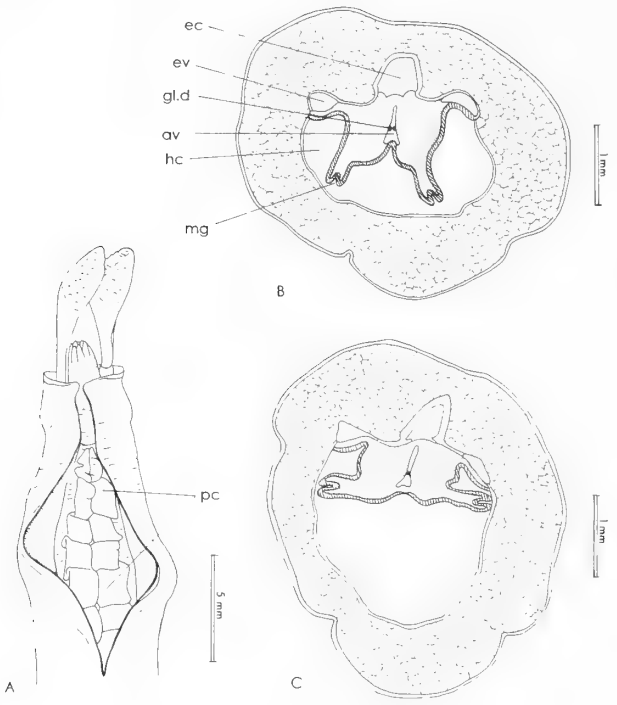

Figure 11

Nausitora fusticula. A. Ventral view, posterior ctenidia (**pc**), after longitudinal incision of the mantle. B and C. Transverse sections of the posterior region of the body of the same animal, to show variation in the disposition of the branchial blades. **av,** afferent branchial vessel; **ec,** epibranchial cavity; **ev,** efferent branchial vessel; **hc,** hypobranchial cavity; **gl. d,** Deshayes gland duct; **mg,** marginal groove.

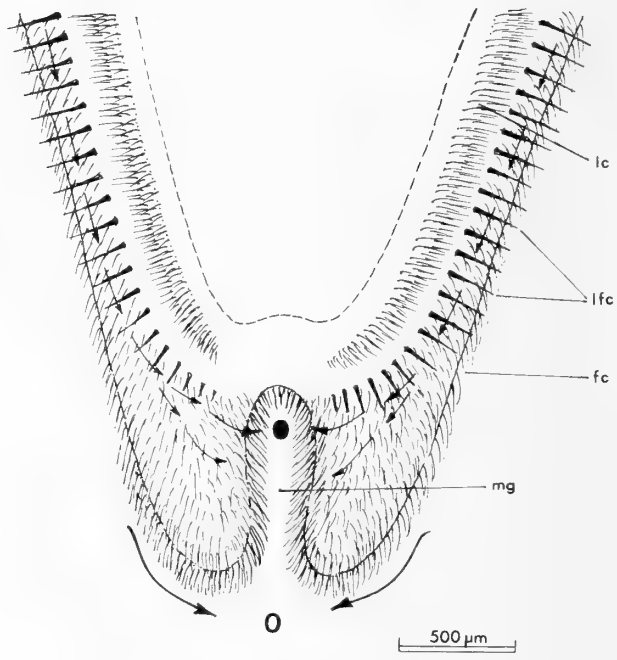

Figure 12

Nausitora fusticula. Lateral view of the free extremity of a filament of the posterior ctenidium. **fc,** frontal cilia; **lc,** lateral cilia; **lfc,** lateral-frontal cilia; **mg,** marginal groove. The arrows indicate the direction of the ciliary currents. "0" indicates the longitudinal currents in anterior direction, external to the marginal groove, and "●" indicates the acceptation current in oral direction.

water currents, which aid in respiration and feeding. On one face of the filament, the waving of these cilia produces a ventrally directed current, and on the other, a dorsally directed one. The lateral-frontal cilia are projected toward the sides of the filaments and alternatively cross with the adjacent filaments, forming a type of grating. These cilia wave from the inside out into the interfilamentar spaces, throwing particles onto the frontal faces of the filament. From here the particles are transported by the frontal cilia, thus avoiding the penetration of large particles into the interior of the demibranchs. The frontal cilia, both on the external and internal blade of each demibranch, conduct particles of different sizes to the ventral region. On arriving at the ventral extremity of the filaments, small particles are diverted by the cilia from the lateral faces toward the interior of the marginal groove, therein being conducted to the anterior region by a strong ciliary current. Larger particles or clumps of small particles are conducted to the anterior region by cilia of the free edge of the demibranch and outside the marginal groove (Figure 12). The cilia of this free edge, even though they are not terminal cilia as observed in other bivalves, function similarly in that they conduct particles to the anterior region through a weak current. The particles in these currents do not, however, arrive at the mouth. Depending on the state of contraction and relaxation of the demibranch, the marginal groove could be distant from or near to the mantle rejection tracts, respectively. When near, the strong ciliary currents of these tracts directly capture particles conducted by the current outside the marginal groove; when far, the agglomerated particles form large masses that fall into the hypobranchial cavity and are collected by the rejection tract.

The quantity of material transported inside the marginal groove is generally small. As excess particles are conducted to the anterior region, they are accumulated, surrounded by mucus, and joined together in large masses, which flow from the inside of the groove. These masses are then retained by the cilia of the rejection tract of the mantle and eliminated.

In the mid and anterior regions of the body, where the ctenidia are reduced to only the marginal groove, all excess material is also prevented from reaching the mouth by a mechanism similar to that described above. Thus the weak selection activity of the ctenidia is compensated for

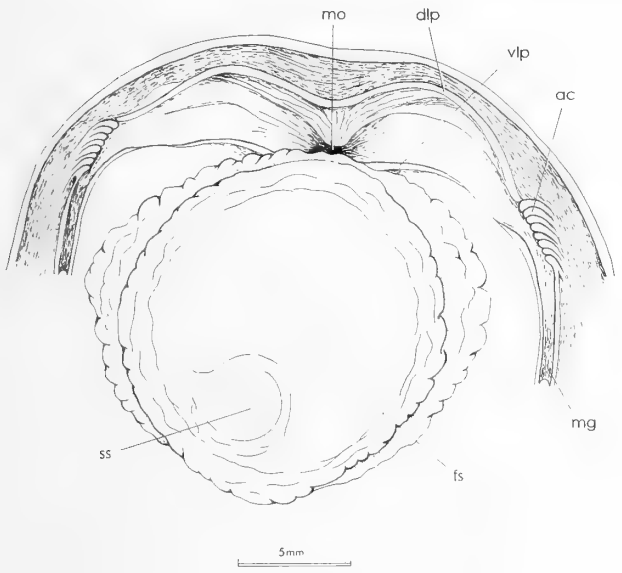

Figure 13

Nausitora fusticula. Frontal view of anterior extremity. **ac,** anterior ctenidium; **dlp,** dorsal labial palp; **fs,** foot sole; **mg,** marginal groove; **mo,** mouth; **ss,** region of the foot where we can see by transparency the extremity of the crystalline style sac; **vlp,** ventral labial palp.

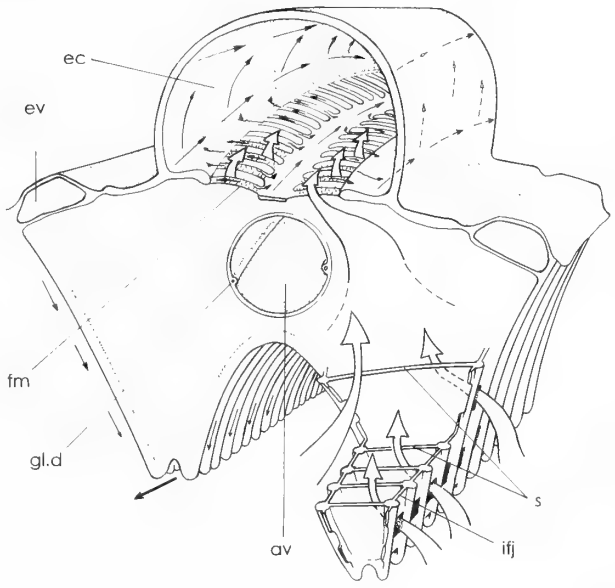

Figure 14

Nausitora fusticula. Diagram of a section of the posterior ctenidium and respective epibranchial cavity, to show water circulation (large arrows) and ciliary currents (small arrows). **av,** afferent branchial vessel; **ec,** epibranchial cavity; **ev,** efferent branchial vessel; **fm,** free edge of the septum; **gl.d,** Deshayes gland duct; **ifj,** interfilamentar junction; **s,** septum of the branchial filament.

by the neamess of its marginal grooves to the rejection tracts of the mantle.

The participation of the ctenidia in the selection of particles is restricted to the free end of the filament where the frontal cilia detour small particles to the marginal groove. The opening and closing of the marginal groove were not observed as control mechanisms of the quantities of particles which remained inside it and were carried to the mouth.

The epithelium of the visceral mass of *N. fusticula,* in the mid-region of the body, presents weak cilia activity which was observed in only a few specimens. In *N. fusticula* the particles in this part of the body are conducted toward the marginal groove.

The ciliary currents in the interior of the epibranchial cavity, which correspond to the posterior ctenidia, are schematically represented in Figure 14, based on histological sections and observations of dissected animals.

The material which comes into this cavity is largely represented by feces coming from the anal canal and by gametes and excretory products. Also, very small particles which have passed the demibranchs enter this cavity. The floor of this region has the appearance of a grate, formed by the most internal portion of the dorsal margin of the interlamellar extensions of the filaments of the two demibranchs. These margins present two types of ciliary currents: one stronger, which directs particles to the sides, the other weaker, which passes the particles to the middle region where the interlamellar extension of one demibranch fuses with that of the other.

The particles transported to the lateral walls of the epibranchial cavity are carried to the posterior body region and simultaneously, to the roof of the cavity until they reach the base of the exhalant siphon through which they are eliminated by means of the exhalant current. The particles that enter into contact with the gutter formed on both sides of the wall of the epibranchial cavity are carried by a strong ciliary current directly to the base of the exhalant siphon.

The particles taken to the mid portion of the epibranchial cavity floor, in most cases, remain stationary and spinning in the same place. Only in the case of one animal was a weak horizontal current detected, carrying the particles to the base of the exhalant siphon.

Beside the ciliary currents on the epithelium, frequent contractions were observed throughout the length of the mantle at the epibranchial cavity. The feces are often eliminated by short and intermittent jets. In this case, the participation of the mantle muscles must be more active, which, on contracting, force out both water and feces in jets. Gametes are continuously eliminated, in which case both the ciliary currents and the flow of the exhalant currents may have a more effective participation.

The anal canal was opened dorsally by a longitudinal

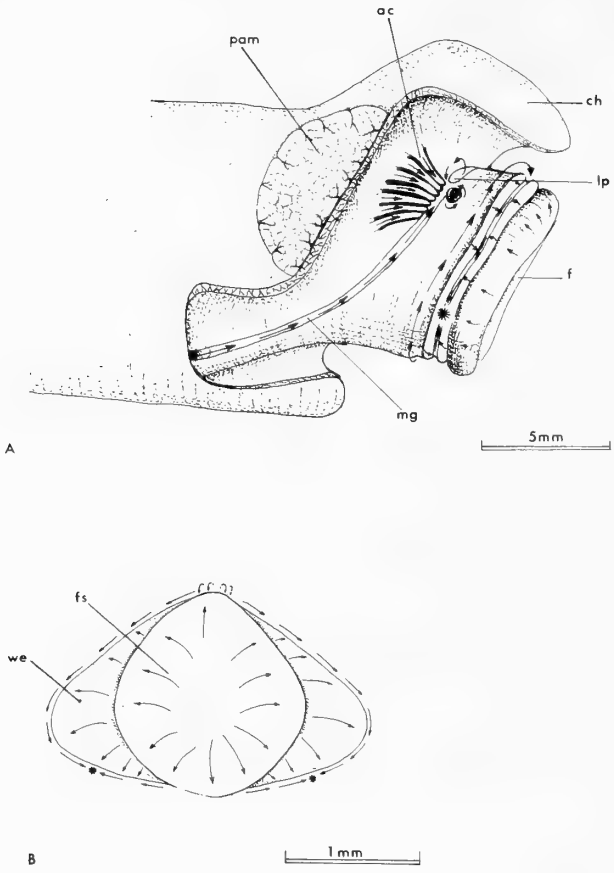

Figure 15

Nausitora fusticula. A. Anterior extremity of the bivalve, viewed from the right side after removal of the shell and part of the mantle. **ac,** anterior ctenidium; **ch,** cephalic hood; **f,** foot; **mg,** marginal groove. B. frontal view of the sole of the foot (**fs**) and of the lateral winged-edge projections (**we**). In A and B, the arrows indicate ciliary currents and the symbol (*) the vortex where particles converge.

incision and the fecal contents were removed. No ciliary activity was detected on its wall.

The epithelium of the foot has an intense ciliary activity in animals in good physiological condition. In unwell animals this activity is reduced or even absent, contrasting with that of the mantle epithelium around the foot, which is always present.

The ciliary currents on the frontal surface of the foot are centrifugal (Figure 15), carrying particles to the ciliated groove which surrounds it. The marginal region of the foot, where this groove is located, can expand, forming on both sides, two winged projections, increasing the perimeter of the foot and lengthening the ciliated groove. The expansion and contraction of these projections do not show a regular rhythm. On the side facing the wood, and on the opposite side of these winged projections, the ciliary currents carry the particles to the marginal ciliated groove. In this groove the particles are carried to the vortex situated ventro-laterally. At this point, particles are accumulated, stuck together with mucus, and captured by the strong rejection tracts of the mantle, moving them toward the inhalant siphon. This considerable ciliary activity contributes significantly to the removal of wood fragments, which originate during gallery boring and are not ingested.

The particles which reach the epithelium just posterior to the ciliated groove of the foot, are carried dorsally until near the mouth, where they enter into contact with the labial palps, or are thrown on the frontal surface of the sole of the foot to be reworked (Figure 15A).

It was very difficult to observe the ciliary currents on the labial palps of *N. fusticula,* due to the small size of the palps. Registration of the ciliary currents was possible only in a few of the specimens examined, and the ciliary activity was not very intense. No movement of particles near the mouth which could be attributed to ciliary activity of the ventral palps was detected.

DISCUSSION

The protractor muscles of the pallets and the retractor muscles of the siphons, in Teredinidae in general, are short and well developed when compared to the retractor muscles of the pallets. They also have both their extremities fixed to hard structures such as the pallet stalk and the calcareous coat of the gallery. The existence of a rigid and firm point of support possibly facilitates quick retraction of the siphons and protraction of the pallets to close the gallery opening when the environment is unfavorable to the animal.

The retractor muscles of the pallets are slender, long, and two of them end by means of very fine branchings immersed in the soft tissue of the mantle. This arrangement could be related to the fact that the retraction of the pallets can be slow and gradual, as it occurs at times when environmental conditions are favorable or non-aggressive.

The behavior of the inhalant siphon of *N. fusticula* demonstrates that the elaborated tentacles and digitiform projections do not act as effective barriers against the penetration of particles into the mantle cavity, but the siphon can regulate the quantity of material that penetrates into the pallial cavity by contracting the circular muscle at the base of the tentacle or withdrawing to the interior of the gallery. Also the ciliary currents of the ctenidia and the efficient rejection tracts of the mantle contribute to the elimination of excess particles as pseudofeces.

Ciliary activity observed on the tentacles of the inhalant siphon is apparently related to the removal of the few small particles which settle thereon. This prevents accumulation of particles on these structures. The rapid retraction and extension movements of the siphons are

probably related to an auxiliary cleaning process of the tentacles, eliminating larger particles which are not removed by ciliary action.

The above cited mechanisms of the inhalant siphon, ctenidia and, rejection tract of the mantle are probably an adaptation of *N. fusticula* to deal with many and slightly dense particles in suspension, as is the case in the environment where the specimens were collected.

According to Turner (1966) and Hoagland & Turner (1981), *N. fusticula* would have returned secondarily to the filtering habit by adding a ciliary plankton filtering mechanism to the tentacles of the inhalant siphon. That supposition was not confirmed in the present work; we observed that ciliary activity on the inhalant siphon tentacles conducted particles to outside the opening.

The sensitivity of the siphons of *N. fusticula* to mechanical stimuli, even of low intensity, is similar to that reported in other teredinids (Quatrefages, 1849; Saraswathy & Nair, 1971). The greater activity of the exhalant siphon in relation to the inhalant one could be related to the participation of the exhalant siphon in the process of pseudocopula, described by Hiroki et al. (1994) for *N. fusticula.* In this process, the exhalant siphon has an active participation in finding and penetration into the exhalant siphon of another animal.

According to Turner (1966), in Teredinidae the length of the posterior ctenidium and the development of the labial palps could be related to greater or lesser importance of plankton as food: species with long ctenidia and more developed palps feed mainly on plankton, the wood being a less important food source to the animal.

The length of the posterior ctenidium of *N. fusticula* can be considered moderate, since it occupies almost 30–40% of the body length. Based on the Turner's supposition, we can say that *N. fusticula* feeds mainly on plankton. On the other hand, the labial palps of *N. fusticula* are very reduced. Morton (1970) believed that the reduced palps in Teredinidae were an adaptation to live in water with few suspended particles. However, according to Purchon (1941), *Teredo norvegica* possesses the most highly developed labial palps among the Teredinidae, while living in turbid waters. *Nausitora fusticula,* living in the same kind of environment, possesses very reduced palps. In this case, the presence of reduced palps could be related to the selective mechanism of the posterior ctenidia and rejection tracts of the mantle, which allows just a small amount of particles to reach the palps and be selected for ingestion.

Within the genus *Nausitora, N. dunlopei* possesses short ctenidia (Turner, 1966) and *N. hedleyi* possesses moderate-sized ctenidia (Saraswathy & Nair 1971) like *N. fusticula.* This suggests that plankton and organic particles might be more important in the nutrition of these two last species than for *N. dunlopei.*

In *N. fusticula,* the anatomy of the ctenidia and their ciliation does not significantly differ from that of other teredinids species described by Ridewood (1903) and Sigerfoos (1908).

The rejection tracts of the mantle in *N. fusticula* are separated throughout their length as was observed by Sigerfoos (1908) in *Xylotrya gouldi* Bartsch, 1908, and by Saraswathy & Nair (1971) in *N. hedleyi.* In *Teredo norvegica* Spengler, 1792, and *Teredo megotara* Hanley, 1848, studied by Purchon (1941) and in *Teredo furcifera* von Martens, 1894, and *Teredora princesae* (Sivickis, 1928), studied by Saraswathy & Nair (1971), these tracts are fused at the posterior body region.

The anterior ctenidium of *N. fusticula* is composed of six to eight filaments, depending on the specimen. This variation is not correlated with the size of the animal. In *Xylotrya gouldi,* the number of filaments is usually nine, rarely 10 or 11 (Sigerfoos, 1908). Some authors, when studying different species, registered a constant number of filaments: Purchon (1941), 10 for *Teredo norvegica* and seven for *Teredo megotara*; Saraswathy & Nair (1971), eight for *Nausitora hedleyi*, and six for *Teredo furcifera.* According to Lazier (1924), there are five filaments in *Teredo navalis,* whereas according to Morton (1970), there are eight. The absence of variation in filament number or the discrepancy among the number of filaments for the same species could be related to small sample size.

Considering the criteria established by Purchon (1939), the filaments of each anterior ctenidium in *N. fusticula* correspond to the ascendent lamella of the demibranch. Ridewood (1903) and Sigerfoos (1908) concluded that, in the species they studied, the filaments of the anterior ctenidium belonged to the descendent lamella of the demibranch. Purchon (1941) contested this conclusion, stating that in the species studied by these authors, the filaments belong to the ascendant lamella of the demibranch. The present study confirms this latter statement.

In *N. fusticula* and in the other estuarine species studied by Saraswathy & Nair (1971) and by Rancurel (1971), there is a well-developed globular structure just posterior to the nephrostoma. This structure, deeply folded and ciliated internally, probably filters the pericardial fluid intensively, contributing to the removal of water and excretion. Perhaps this structure occurs only in estuarine species where the salinity is lower and more variable than in ocean waters.

Comparing the major anatomical characters described in the present work for *N. fusticula* with that of *N. dunlopei* described by Turner (1966), and *N. hedleyi* described by Saraswathy & Nair (1971), we can conclude that *N. fusticula* differs from *N. hedleyi* and *N. dunlopei* by the pallets, the presence of tentacles around the inhalant siphon, and the deep marginal groove in the posterior ctenidium. In addition, *N. fusticula* differs from *N. dunlopei* by the position of the gonads posterior to the appendix, as well as by the reduced length of the appendix and the bigger extension of the posterior ctenidia.

ACKNOWLEDGMENTS

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The Veliger 41(3):289–293 (July 1, 1998)

THE VELIGER

NOTES, INFORMATION & NEWS

Redescription of the Aeolid Nudibranch *Flabellina ischitana* Hirano & Thompson, 1990 (Gastropoda: Opisthobranchia)

by
Juan Lucas Cervera,[1] Pablo José López-González,[2] and Jose Carlos García-Gómez[2]
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Samples from the southwestern Iberian Peninsula coast have permitted us to examine several specimens of *Flabellina* Voigt, 1834, identified initially as juveniles of *F. affinis* (Gmelin, 1791). However, a more detailed study of these specimens has shown them to be the recently described species. *Flabellina ischitana* Hirano & Thompson, 1990. We describe additional anatomical features in order to complete the descriptions of these species.

SYSTEMATICS

Family FLABELLINIDAE Bergh, 1889

Genus *Flabellina* Voigt, 1834

Flabellina ischitana Hirano & Thompson, 1990

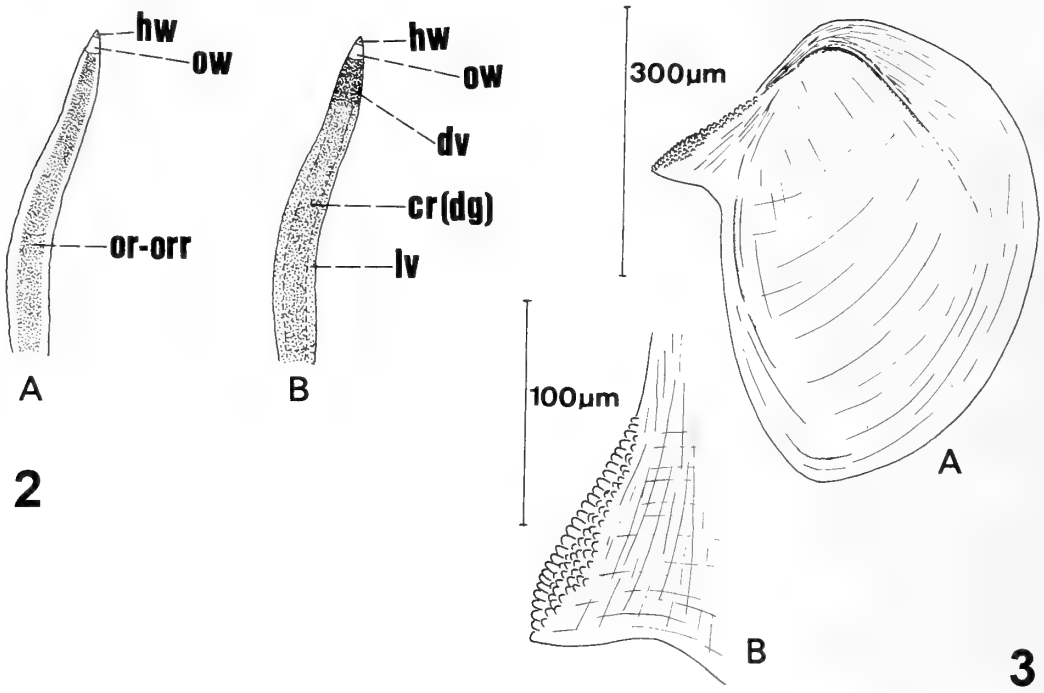
(Figures 1–7)

Material examined: Compañia Española de Petróleos, S. A. harbor, Bay of Algeciras (Cádiz), Strait of Gibraltar (36°11′07″N; 5°23′08″W): 4 specimens of 15 to 20 mm in length, collected at 5 to 10 m depth on *Eudendrium racemosum* (Cavolini, 1758) (March 1994). Santa María del Mar beach, Cádiz. southwestern Iberian coasts (36°31′N; 6°17′W): 2 specimens of 5 mm in length, collected from the intertidal zone, under stones (December 1993). All specimens are deposited at the collections of the Laboratorio de Biología Marina of the University of Sevilla, Spain (LBM), which does not assign individual lot numbers.

Description: The general body color, including the rhinophores, oral tentacles, and ceratal bases is violet, though the apical region of oral tentacles and rhinophores is opaque white. The branches of the digestive gland can

Figure 1

Flabellina ischitana. External morphology of one specimen of 35 mm in length.



Explanation of Figures 2 and 3

Figure 2. A. Coloration of a ceras of *Flabellina ischitana.* B. Coloration of a ceras of *F. affinis.* Key: cr(dg), cream digestive gland; dv, dark violet; hw, hyaline white; lv, light violet; or-orr, orange-orange red; ow, opaque white.
Figure 3. *F. ischitana.* A. Jaws. B. Detail of the masticatory border of the jaw.

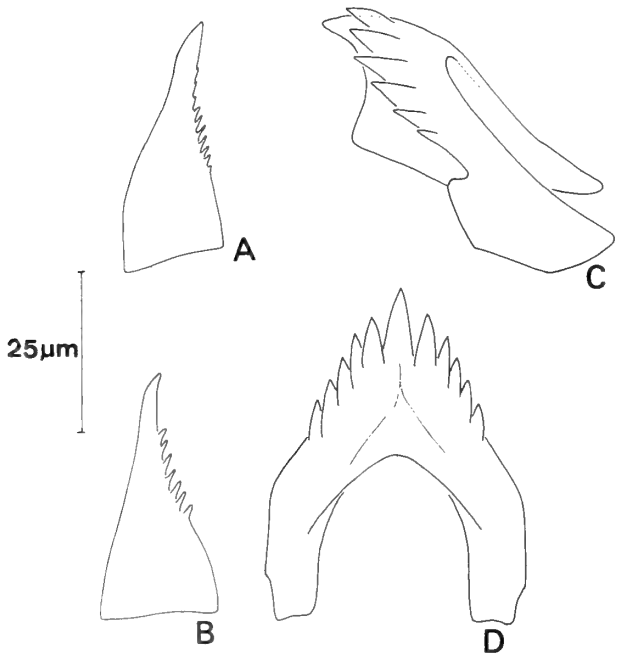


Figure 4

Flabellina ischitana. A & B. Lateral radular teeth. C. Lateral view of the rachidian tooth. D. Doral view of the rachidian tooth.

be seen through the skin of the cerata (Figure 2A). Their color is orange to red-orange. The subapical zone of the cerata has an opaque white ring that partially obscures the cnidosacs, while the apex is hyaline white. The foot sole is whitish. The body is elongate, with 5–15 ceratal groups per side. Each group inserts on a stalk and has numerous cerata which vary in number between seven to nine in the more anterior groups to only one in the most posterior group. The cerata are long and slender. The corners of the foot are curved and prominent. The rhinophores usually are annulate (8–12 lamellae), but they can be also simply rough, without well-defined annulli. The oral tentacles are elongate and similar in size to the rhinophores. The genital pore opens at the right side, in front of the first group of cerata, while the anus opens between the first and the second groups, in a pleuroproctic position. The pericardium is situated between the first and the second groups of cerata. The tail is long and pointed.

The jaws are ovoid and transluscent, with a denticulate masticarory border with several distinct rows of denticles (Figures 3A, B; 5A, B). The radular formula in a 20 mm specimen is 21 × 1.1.1. The rachidian tooth has a well-developed depressed central cusp and five to six strong denticles on either side of it. The narrow lateral teeth have up to eight to nine more or less prominent denticles (Figures 4A, D; 5C, E). The genital system (Figure 6) has a

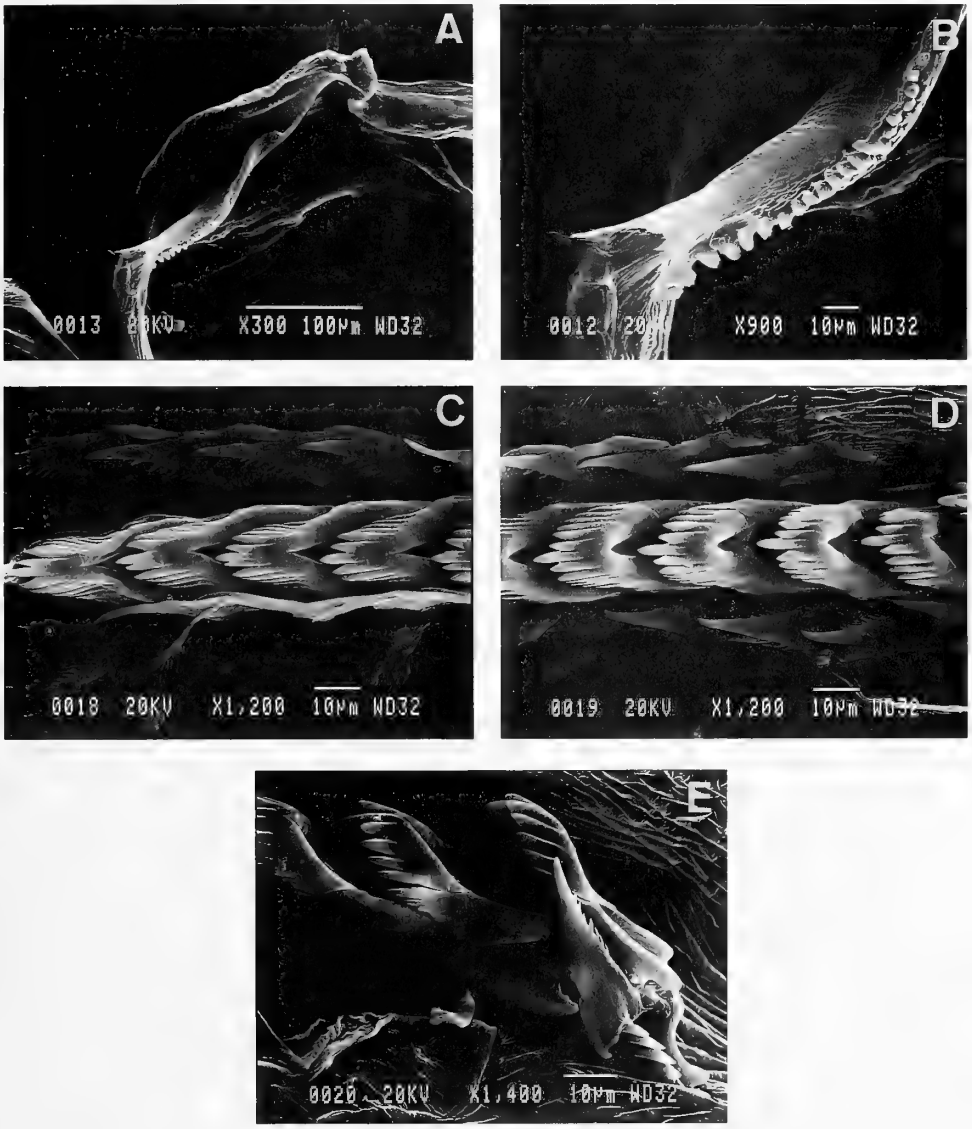


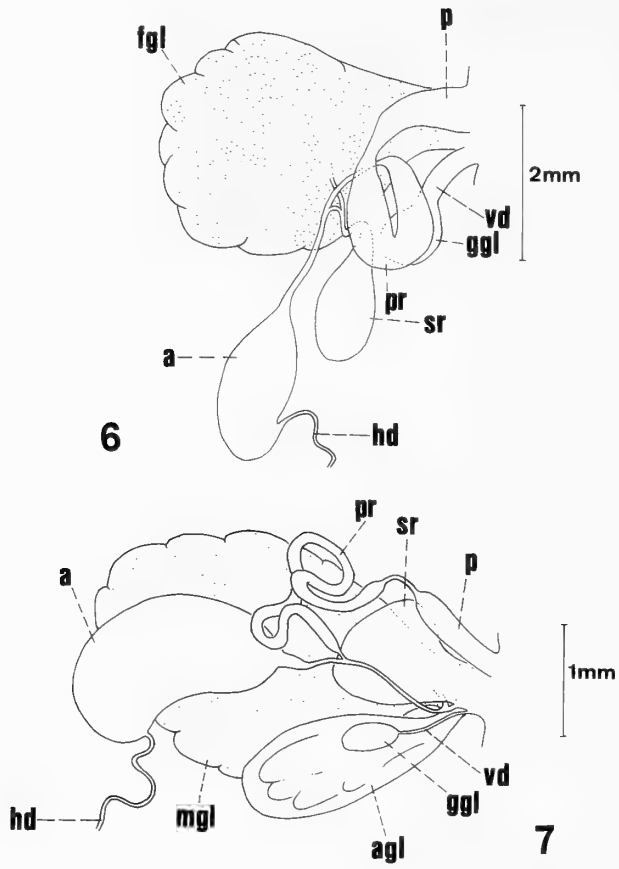
Figure 5

Flabellina ischitana. Scanning electron micrographs. A & B. Details of the masticatory border of the jaws. C, D & E. Details of the radular teeth.

large, ovoid hermaphroditic ampulla that continues as a relatively long deferent duct, which is wide along two-thirds of its length. This portion corresponds to the prostatic part, which folds over itself once, before joining the penis. The seminal receptacle is pyriform and large, while the gametolytic gland is rounded and smaller than the former. There is a thick and relatively short vaginal duct.

Distribution: *Flabellina ischitana,* described originally from specimens collected from the Gulf of Naples (Hirano & Thompson, 1990), has been also recorded in Northern Sardinia (Cattaneo-Vietti et al., 1990) and along the Mediterranean coasts of Spain (Almería) (García-Raso et al., 1992). Our specimens constitute the westernmost record of the species and the first in Atlantic waters. It is probable that many earlier records attributed to *F. affinis* (Gmelin, 1791) along the European coasts, before the description of *F. ischitana,* should be attributed to the latter species and not to the former. For example, this is the case of those of Cervera & García (1986) and Cervera et al. (1988) for the western Andalusian coasts.

Remarks: The species most similar to *Flabellina ischitana* is *F. affinis* (Gmelin, 1791). These two could be confused easily. Hirano & Thompson (1990) described the differences between both species. In *F. ischitana* the



Explanation of Figures 6 and 7

Figure 6. *Flabellina ischitana.* Reproductive system. Figure 7. *F. affinis.* Reproductive system. Key: a, ampulla; agl, albumen gland; fgl, female gland; ggl, gametolytic gland; hd, hermaphroditic duct; mgl, mucus gland; p, penis; pr, prostate; sr, seminal receptacle; vd, vaginal duct.

ceratal surface is translucent, without violet coloration. In *F. affinis,* the zone immediately under the subapical opaque white ring has another dark violaceous ring which obscures the digestive gland. This detail allows us to distinguish the species externally, even in preserved animals (Figure 2A, B). According to Hirano & Thompson (1990), the lateral teeth of *F. ischitana* usually lack denticles (only one specimen of their material had three to five tiny denticles). However, our specimens have very well developed denticles, even more so than in *F. affinis.* It could be that the teeth observed in the specimens examined in the original description were never formed or are not typical of the normal form of the teeth. Moreover, the basal zone of the lateral teeth is clearly wider in *F. affinis* than in *F. ischitana.* The most important difference observed between the reproductive systems of our specimens and those described by Hirano & Thompson is the considerably larger size of the seminal receptacle, vaginal duct, and gametolytic gland. Perhaps, the specimens on which the original description of the reproductive system was based were collected in a nonreproductive period. In spite of these differences, the arrangement of the reproductive system of our specimens is the same of those of Hirano & Thompson (1990) and those specimens of "*F. affinis* with an aberrant reproductive system" (probably belonging to *F. ischitana*) described by Schmekel (1970) and Schmekel & Portmann (1982). In order to compare the reproductive system of the above cited species, four specimens of *F. affinis* (30–35 mm in length, at 10–12 m depth on *Eudendrium* sp., Tarifa, Strait of Gibraltar, southern Iberian Peninsula, July 1994) were examined (these specimens were deposited at the collections of the LBM). If we compare the arrangement of the reproductive systems of *F. ischitana* (Figure 6) and *F. affinis* (Figure 7), differences between both species can be observed. The latter species has the vaginal duct joining the duct of the seminal receptacle, while the duct of the seminal receptacle of the former enters the female gland, and no connection with the vaginal duct has been observed. Moreover, the prostate in *F. ischitana* is thicker and shorter than in *F. affinis.* The egg masses of these two species are also different, since they are pinkish to violaceous in *F. affinis* and white in *F. ischitana.*

Acknowledgments

We are deeply grateful to César Megina for his help in several aspects of this work and Drs. T. M. Gosliner and A. Medina for their valuable comments on the manuscript. We also thank Mr. Juan González from the Servicios Centralizados de Ciencia y Tecnología de la Universidad de Cádiz for supplying facilities for the scanning electron photographs. This paper has been supported by the project "Fauna Ibérica III" (DGICYT PB92-0121), as well as by the Compañia Española de Petróleos. S. A. (CEPSA), the Compañia Sevillana de Electricidad, the Excmo. Ayuntamiento de Los Barrios, and the Mancomunidad de Municipios del Campo de Gibraltar through the project "Estudio biológico de la Bahía de Algeciras."

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THE VELIGER

The Veliger 41(3):293–296 (July 1, 1998)

BOOKS, PERIODICALS & PAMPHLETS

Mollusca: The Southern Synthesis
Fauna of Australia, Volume 5

edited by P. L. BEESLEY, G. J. B. ROSS & A. WELLS, with contributions by 70 authors. 1998. Published by CSIRO Publishing, Melbourne. xiv + 1234 pp. in two volumes. ISBN 0-643-05756-0. Available from CSIRO Publishing, P.O. Box 1139, Collingwood, Victoria 3066, Australia; may be ordered from home page http://www.publish.csiro.au.

Mollusca: The Southern Synthesis is the malacological component of the *Fauna of Australia,* an amibitious project that aims to provide authoritative syntheses of the primary zoological literature on all Australian taxa, to the level of generality expressed by what canonical systematics calls the family.

It is described, without exaggeration, as "the most comprehensive and authoritative treatment yet" of Australia's mollusks, with contributions from over 70 international authors (mentioning some of their names here would slight the contributions of others), 200 color and 500 black and white photographs, over 2500 line drawings, targeted for "a broad non-specialist readership, including ecologists, biologists, paleontologists, conservationists, land managers, and senior secondary and tertiary students." This somewhat understates the usefulness of the work, because it will be a valuable resource for molluscan specialists as well.

The price—$295 US ($295 A), plus shipping and handling—undoubtedly means there will be more institutional than individual buyers. Without denigrating the contribution of the authors and compilers, which deserves to be compensated—no doubt much more richly than it has been—I would still suggest that an educational committee, somewhere, should address the question of how to get a comprehensive overview of the Mollusca into the hands of the ordinary citizen for less than 300 bucks.

It would take a committee to evaluate all parts of the work in detail. A thoughtful review from a traditional systematist's point of view has appeared recently in a shell club publication (McLean, 1998) and on the MOLLUSCA Internet list (archived at http://www.ucmp.berkeley.edu/mologis/mollusca.html; search on keywords "southern synthesis" using the quotation marks). Many of its well-taken points need not be repeated here. McLean notes that dates and authorship are left off the names of taxa. That probably makes smoother reading for the "broad non-specialist readership"; but practicing taxonomists will miss the convenience of authors and dates.

A second and more serious problem stems from the fact that the work inhabits a kind of nether world between being a strictly Australian manual and a truly worldwide resource. The in-depth treatment of general biology and natural history transcends regional boundaries. Much of the information on widespread (i.e., not merely Australian) taxa is based on studies of mollusks from other regions. Because of its scope and depth, *The Southern Synthesis* bids fair to become the *de facto* global sourcebook on matters molluscan. But workers who adopt it for more than regional purposes do so at their own risk. (Whether or not this is fair payback for previously Eurocentered texts such as Woodward's *Manual of the Mollusca* could be debated at length down at the local Malacologists' Tavern.)

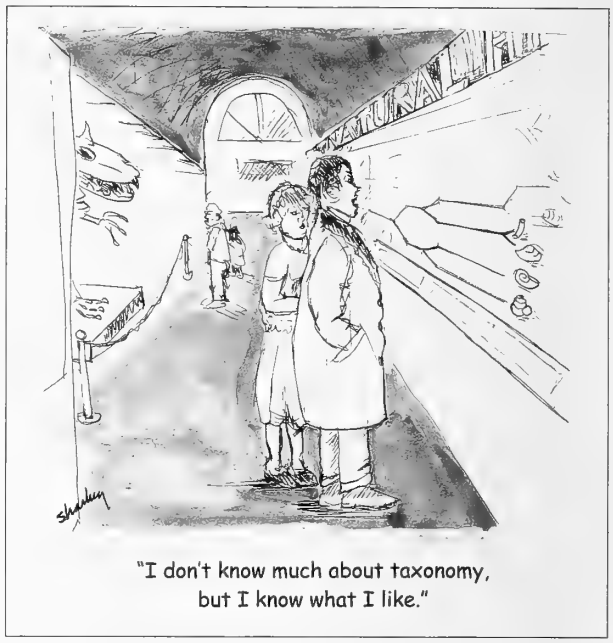
It is quite likely, for instance, that the classification will be adopted for many personal and institutional reference collections and as a schema for course outlines at various levels. This is anticipated by the inclusion in the work of a separate, loose-leaf classification chart. From the viewpoint of pulmonate systematics (my specialty), that would be a decidedly retrograde step. Except for the use of standard "-oidea" endings for superfamily names and some diddling with ranks, the pulmonate taxonomy is basically the Australian subset of the classification of Solem (1978), the most conservative of recent classifications of stylommatophoran land snails (Emberton et al., 1990). From this work, one could not guess the existence of the Humboldtianidae, the probable sister-group of the Helicidae, which together compose a major Laurasian clade. One would conclude that the Hygromiidae, Helicodontidae, and other taxa accepted by practically all serious

modern authors had been folded back into Helicidae. The existence of Xanthonychidae, critical to the estimation of helicoid biogeography worldwide, would remain a mystery. "Tough, mate," perhaps; but an informed user will know that there is more to the story than we are given here.

Absence of the hot-vent gastropod taxa—a deeply rooted although non-holophyletic group in the hypothesis of Ponder & Lindberg (1997)—is a serious lack, if not to Australian "land managers," then certainly to "senior secondary and tertiary students."

With more than 70 authors, the work necessarily represents a collage of different assumptions and styles of analysis. Although the editors have normalized the various contributions on the procrustean bed of formal ranking, the components are still a mixture and not operationally intercomparable. For example, portions of the pulmonate land snail part were written by the late Alan Solem, which means that they were compiled before 1990. A lot of interesting pulmonate taxonomy has been done since then.[1] Solem never accepted cladistics, let alone phylogeny-based taxonomy, and he had only uncomplimentary words to say about them (e.g., Records of the Western Australian Museum, Supplement 43:991). By contrast, the section on Patellogastropoda by D. R. Lindberg is based on cladistic analyses and its component taxa are all monophyletic units.

The systematics of *The Southern Synthesis* is resolutely rank-driven. Even the Lindberg classification of the Patellogastropoda, originally submitted as a rank-free taxonomy based on his phylogenetic hypothesis (figure 15: 31), has formal rank headings patched in by the editors. So the *Synthesis* endorses the popular fiction that formal ranks have some transcendent significance, other than the scope we have grown comfortable with through usage. It may be that somewhere in the bowels of the Commonwealth Scientific and Industrial Research Organization is a memorandum that decrees "the taxa of animals shall be categorized according to the formal ranks Class, Subclass, Superorder, Order, Infraorder [. . .] and such other formal ranks as shall be found necessary to keep said taxa in their rightful places." Or perhaps this edict exists only in the minds of canonical systematists. But formal ranks are merely useless gold braid. The authors of the introduction to the prosobranchs (mercifully, that paraphyletic group is not treated as a formal taxon) note that the ranks of taxa are purely arbitrary and that "differences in rank [i.e., between one classification and another] are unimportant—what matters is the relationship of the taxa, that is their relative positions on a phylogenetic tree" (p. 609). This is not only true but is the heart of the argument for rank-free taxonomy; in the midst of a 1200-page rank-filled tome it is rather a wee voice in the wilderness.



"I don't know much about taxonomy, but I know what I like."

Canonical systematists claim that formal ranks are necessary to help them (or unspecified straw-person "workers") negotiate their way around the taxonomy of mollusks. McLean (1998:49), for instance, suggests "that phylogeneticists deal with the problem of ranking as best they can (by not naming every branch of the tree, for example) and produce ranked classifications that can be visualized and more readily understood." This peculiar sentence conflates at least two concepts: (1) the use of formal ranks, and (2) which subdivisions of a hierarchic taxonomy to name. Typical of canonical systematists (cf. Schander & Tholleson, 1995; and figure, above), McLean, while recognizing that ranking is a problem, rejects rank-free taxonomy but offers no concrete alternative proposal.

Likewise, with regard to "naming every branch of the tree," McLean makes no specific suggestions as to which branches should be named. In my phylogenetic analysis of Helminthoglyptidae (Roth, 1996), I named every taxon down to the least inclusive level considered in the analysis (mostly a genus or subgenus of traditional usage); although that was done partly for heuristic reasons, I have not yet had any occasion to regret it. The unspoken point of complaints like McLean's seems to be "too many names," but I don't think number of names is really a problem—at least not for persons literally *using*, not just

[1] I would point particularly to the work of Scott (1996, 1997), which impacts on the Australian fauna. Although this work can be criticized with regard to the character set and the array of taxa analyzed, and other workers and I have been unable to replicate her results, even using the published data matrix and HENNIG86 settings, the articles ask the right questions and use appropriate methods to address them.

totting up, the taxa of a classification. One's working vocabulary expands readily to accommodate nouns in active use.

A more serious problem (and one not limited to phylogenetic taxonomy) is evanescent names. In active periods of phylogenetic investigation, a given phylogenetic hypothesis may last only until the next publication, and some taxa based on it (even with explicit phylogeny-based definitions, e.g., "SONORELLAMORPHA consists of *Sonorella hachitana* and all taxa that share a more recent common ancestor with it than with HELMINTHOGLYPTAMORPHA") may become absurd or redundant units. I therefore suggest that, if it is desired to limit the names in a phylogenetic taxonomy, the units chosen for naming be those that survive at a certain level of clade-decay analysis. The critical value will be arbitrary, but interested parties could probably agree on some round number. The clades meeting this criterion will be those that are best supported by the underlying data and thus can reasonably be expected to stand up in the face of future new data and analysis. They will not, of course, necessarily be the groups recognized by traditional taxonomy. The clades that do not meet the criterion can simply be referred to by their components, e.g., "*Cryptomastix+Trilobopsis*" for clade "C+Q" of Emberton (1994, fig. 5). This is another case in which the protocols of cladistics provide, if not a completely objective, at least an explicit basis for nomenclatural practice, something canonical systematics has continually resisted.

B. Roth

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The Recent Molluscan Marine Fauna of the Islas Galápagos

by KIRSTIE L. KAISER. 1997. The Festivus 29 (Supplement, December 4, 1997): iii + 67 pp. Soft cover, 215 × 280 mm.

This work represents the latest important contribution to the knowledge of the molluscan marine fauna of the Galápagos Islands, by Kirstie Kaiser, Museum Associate of the Los Angeles County Museum of Natural History, and is her second major publication on this topic, after the overview of the micromolluscan species of the archipelago (Kaiser, 1993). It is not illustrated, except for the beautiful cover, figuring the H.M.S. *Beagle* sailing in view of the Galápagos, from a painting by J. Chancellor.

After some explanatory paragraphs (Introduction, Materials & Methods, Discussion, and Results), four tables and an updated faunal list in the form of an Appendix are provided. The bibliography lists 297 references, with 81 of them not previously cited in the documented faunal list by Finet (1994). An index to the taxa ends the publication.

The first table draws up an inventory of the deep-water taxa, with depth range indicated for each species. The second table brings our knowledge of the fauna up-to-date by enumerating additional taxa not listed or not yet considered of verified occurrence in Finet (1994). Table 3 stresses the species previously listed as endemic (Finet, 1994), and now known to be no longer restricted to the Galápagos. Table 4 is an abbreviated census giving number of species in each category.

The faunal list is divided in two parts, one for the accepted species (Appendix 1), and a second for the mollusks excluded from the Galapagan fauna (rejected records, Appendix 2). The list of accepted taxa includes 846 species i.e., theoretically 128 more than in the faunal list by Finet (1994), although there seems to be an inexplicable discrepancy between this number and a count that would result from the contents of Table 2, nor does it match exactly the author's count of 84 bivalves, 41 gastropods, and 4 cephalopods. Also, the list of accepted species includes several entries unidentified or with a questionable identification.

Each entry of the faunal list includes species number used in Keen (1971) when available, species status (endemic, deep-water, etc.), a selection of published Galá-

pagan records with authors and dates for references, and in some cases catalog numbers of museum-examined material (mainly from the Los Angeles County Museum). The bibliographical references mentioned for a species generally include the initial published Galápagan record, and sometimes a few other reported citings, including those in Finet (1985, 1991, 1994), as well as additional earlier citations not mentioned in Finet (1994), if any.

Species additions to the list of Finet (1994) or confirmations of species previously listed as of doubtful occurrence are eventually documented by museum references or locality data. All species previously validated by Bernard, McKinnell & Jamieson (1991) are included in the list of accepted species. For those species no longer considered endemic, records from other localities are also documented.

The list of rejected species (Appendix 2) is similarly annotated and is largely traced out from Finet's documented list of species of doubtful occurrence (1994).

Species are arranged in taxonomic order according to Keen (1971), but recent taxonomic changes are taken into account. Some entries include a subgeneric designation, but most of them do not.

Addition of new taxa to the verified Galápagan fauna, combined with a recognized wider distribution for species earlier believed to be restricted to the Archipelago, contributes to diminish the proportion of the endemic fraction of the fauna. Kaiser points out that from a total of 142 species listed as endemic by Finet (1994), the number has now been reduced to 125, a decrease of 12% from what was counted in 1994. Of these 125 species, 39 are considered from deep water and consequently 86 from shallow water.

Unfortunately, the author does not calculate the new percentages of endemic species. Her new data would show that the overall percentage of endemic species becomes about 15% (compared to 20% in Finet, 1994), while among the shallow-water species alone, 11% only are now considered endemic (compared to 16% in Finet, 1994).

This work complements the previous studies, inventories, and faunal lists of the marine mollusks of the Galápagos by increasing the census of the malacological component in the Archipelago with many new records of species, hence improving significantly our knowledge of this fauna. Although being essentially a compilation built upon another compilation, that of Finet (1994), it is certainly a most useful summary for those working on the eastern Pacific and Galápagan malacofaunas.

It is also encouraging to witness such a revival of interest in the Galápagos marine mollusks, with more malacologists becoming involved, which may result in a more comprehensive insight into the Galápagos marine biodiversity.

Yves Finet

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Manuscripts must be typed, one side only, on A4 or equivalent (e.g., 8½″ × 11″) white paper, and double-spaced throughout, including references, figure legends, footnotes, and tables. All margins should be at least 25 mm wide. Text should be ragged right (i.e., not full justified). Avoid hyphenating words at the right margin. Manuscripts, including figures, should be submitted in triplicate. The first mention in the text of the scientific name of a species should be accompanied by the taxonomic authority, including the year, if possible. Underline scientific names and other words to be printed in italics; no other manipulation of type faces is necessary on the manuscript. Metric and Celsius units are to be used. For aspects of style not addressed here, please see a recent issue of the journal.

The Veliger publishes in English only. Authors whose first language is not English should seek the assistance of a colleague who is fluent in English before submitting a manuscript.

In most cases, the parts of a manuscript should be as follows: title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, figure legends, footnotes, tables, and figures. The title page should be a separate sheet and should include the title, authors' names, and addresses. The abstract should be less than 200 words long and should describe concisely the scope, main results, and conclusions of the paper. It should not include references.

Literature cited

References in the text should be given by the name of the author(s) followed by the date of publication: for one author (Phillips, 1981), for two authors (Phillips & Smith, 1982), and for more than two (Phillips et al., 1983). The reference need not be cited when author and date are given only as authority for a taxonomic name.

The "literature cited" section should include all (and only) references cited in the text, listed in alphabetical order by author. Each citation must be complete, with all journal titles ***unabbreviated,*** and in the following forms:

a) Periodicals:

Hickman, C. S. 1992. Reproduction and development of trochacean gastropods. The Veliger 35:245–272.

b) Books:

Bequaert, J. C. & W. B. Miller. 1973. The Mollusks of the Arid Southwest. University of Arizona Press: Tucson. xvi + 271 pp.

c) Composite works:

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117–135 in R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), Intertidal Invertebrates of California. Stanford University Press: Stanford, Calif.

Tables

Tables must be numbered and each typed on a separate sheet. Each table should be headed by a brief legend. Avoid vertical rules.

Figures and plates

Figures must be carefully prepared and submitted ready for publication. Each should have a short legend, listed on a sheet following the literature cited. Text figures should be in black ink and completely lettered. Keep in mind page format and column size when designing figures. Photographs for halftone reproduction must be of good quality, trimmed squarely, grouped as appropriate, and mounted on suitably heavy board. Where appropriate, a scale bar may be used in the photograph; otherwise, the specimen size should be given in the figure legend. Photographs should be submitted in the desired final size.

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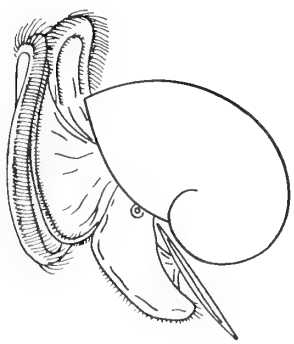

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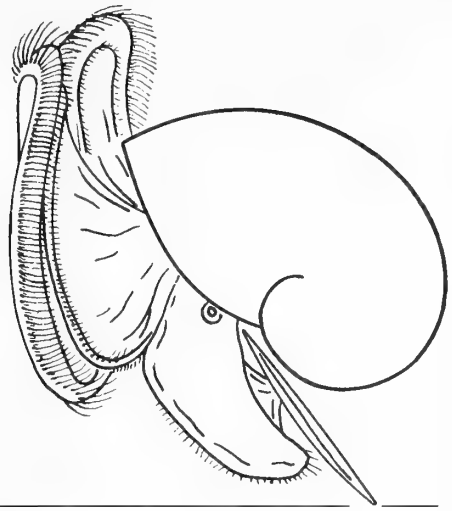
THE VELIGER



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The Veliger is an international, peer-reviewed scientific quarterly published by the California Malacozoological Society, a non-profit educational organization. *The Veliger* is open to original papers pertaining to any problem connected with mollusks. Manuscripts are considered on the understanding that their contents have not appeared, or will not appear, elsewhere in substantially the same or abbreviated form. Holotypes of new species must be deposited in a recognized public museum, with catalogue numbers provided. Even for non-taxonomic papers, placement of voucher specimens in a museum is strongly encouraged and may be required.

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THE VELIGER

The Veliger 41(4):297–313 (October 1, 1998)

New Information on Morphology, Stratigraphy, and Paleoclimate Implications of the Eocene Brackish-Marine Gastropod *Loxotrema turritum* Gabb, 1868, from the West Coast of the United States

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Abstract. New morphologic information about the aperture of the brackish-marine Eocene gastropod *Loxotrema turritum* Gabb, 1868, allows for reassignment of this species from family Thiaridae to family Melanopsidae and shows that *L. turritum* is most closely related to the melanopsid *Faunus ater* Linnaeus, 1758, found today in the fully tropical Indo-West Pacific region near the mouths of rivers. New stratigraphic and geographic data show that the earliest record of *L. turritum* is in lowermost Eocene ("Meganos Stage") rocks in northern California, and that the species was most widespread during the middle lower Eocene ("Capay Stage") when it ranged from southern California to as far north as Crescent Bay, Washington. Most of these "Capay Stage" specimens underwent downslope postmortem transport, most likely from deltaic areas, into deeper waters and became mixed with shallow-marine mollusks. The "Domengine Stage" record of this species is known only from California. From the middle part of this stage (lowermost middle Eocene) through the end of the geologic range of this species in the lower part of the "Tejon Stage" (lower middle Eocene), *L. turritum* lived in brackish-marine lagoons or bays within deltaic complexes in southern California. The last records of this species help confirm data from other disciplines that during the early middle Eocene there was a climate change from humid to drier conditions.

INTRODUCTION

The brackish-marine gastropod *Loxotrema turritum* Gabb, 1868, the only known species of genus *Loxotrema* Gabb, 1868, is confined to lower and lower middle Eocene rocks on the west coast of the United States. This article, which represents the first detailed study of any Eocene brackish-marine mollusk from the west coast of the United States, contains a thorough review of the stratigraphic occurrences and inferred depositional environments of this species. In addition, it contains the first discussion of the paleoclimatic implications of this species.

Loxotrema turritum is very distinctive due to its tabulate whorls and large cylindrical body whorl, but specimens are prone to poor preservation of the outer lip and the anterior end of the aperture, as evidenced by nearly all the published illustrations of this species. These features, which are critical in determining familial assignment, have not been used before by other workers, who, on the basis of general morphology, traditionally placed *Loxotrema* in the family Thiaridae. I examined nearly 300 specimens of *L. turritum,* most of which are stored at several museums on the west coast. I found only a single individual that shows the entire aperture and only two individuals that show some indication of protoconch morphology. This new morphological information reveals that *L. turritum* is most closely related to the extant melanopsid *Faunus ater* Linnaeus, 1758.

While examining museum collections, I found new stratigraphic and geographic occurrences of *L. turritum.* The known geologic range of this species is now lowered to the earliest Eocene, and its known geographic range is now extended northward to the Olympic Peninsula of southwestern Washington (Figures 1, 2).

Since the early paleontologic work by Arnold (1909) in the coal-bearing district of Coalinga in central California, *L. turritum* Gabb, 1868, has been recognized as a component of brackish-marine molluscan assemblages of Eocene rocks of California. Until this present article, however, there has been no attempt to evaluate all of its inferred depositional environments. As will be discussed herein, most of the early Eocene specimens of *L. turritum* were prone to displacement from coastal waters into much deeper waters, whereas middle Eocene specimens are usually found nearly *in situ* in deltaic settings. The species lived for 8.5 million years in humid, tropical to subtropical conditions. The disappearance of *L. turritum* from the fossil record during the early middle Eocene helps confirm data from other sources (paleosols, clay minerals, megaflora, palynomorphs, land-mammals, and land snails) that there was a change in climate at that time to drier conditions.

In this article, the term "shallow-marine" refers to unrestricted, nearshore waters of normal-ocean salinity seaward of beaches or barrier bars. The term "brackish-marine" refers to restricted waters with salinities lower than

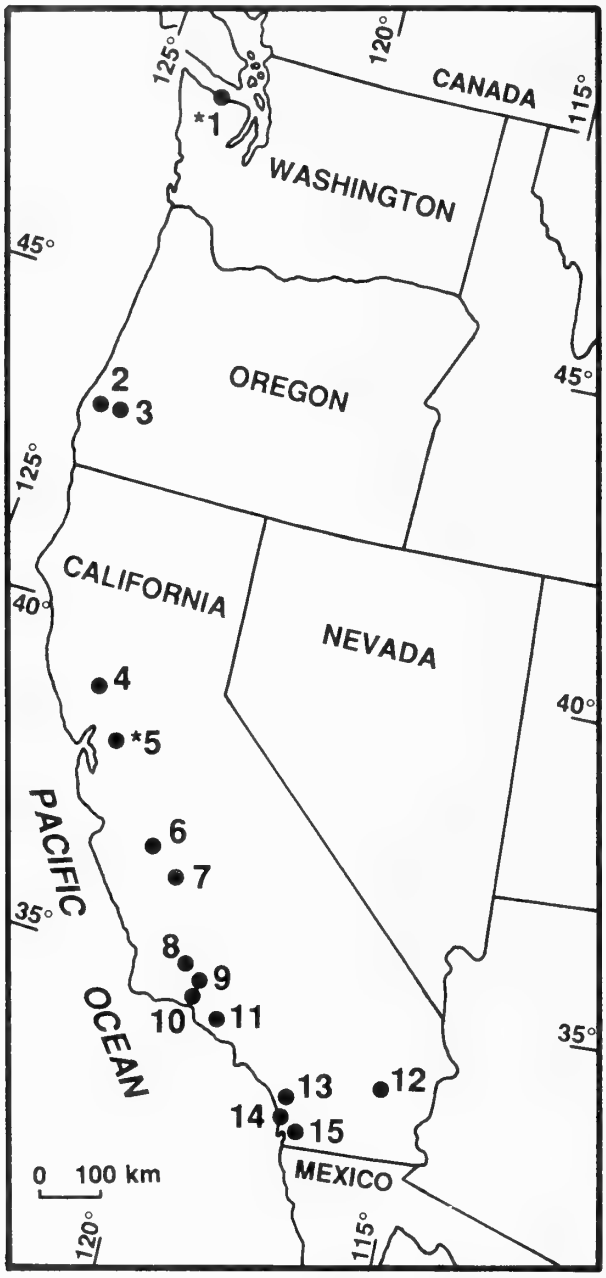

Figure 1

Index map showing geographic locations of *Loxotrema turritum* Gabb, 1868. Locations are numbered from north to south. (1) Crescent Bay. (2) West of Roseburg. (3) Glide. (4) Smith Canyon. (5) Kellogg Creek. (6) Griswold Canyon. (7) Coalmine Canyon. (8) Mouth of Alamo Creek and Beartrap Canyon areas. (9) Pine Mountain. (10) Matilija Hot Springs. (11) Simi Valley. (12) Orocopia Mountains. (13) Vista. (14) Torrey Pines State Reserve and Blacks Canyon areas. (15) Murphy Canyon. (* = New report).

those of normal-ocean waters. Furthermore, the term "brackish-marine" refers to waters landward of beaches or barrier bars but with some connection to the shallow-marine environment.

The following institutional acronyms are used: CAS, California Academy of Sciences, San Francisco; CSUN, California State University, Department of Geological Sciences, Northridge; LACM and LACMIP, Natural History Museum of Los Angeles County, Section of Malacology and Invertebrate Paleontology, Los Angeles, respectively; SDSNH, San Diego Society of Natural History; UCMP, University of California Museum of Paleontology, Berkeley; and UCR, University of California, Riverside.

SYSTEMATIC PALEONTOLOGY

Superorder CAENOGASTROPODA Cox, 1959

Order NEOTAENIOGLOSSA Haller, 1882

Superfamily CERITHIOIDEA Férussac, 1819

Family MELANOPSIDAE Adams & Adams, 1854

Discussion: The family Melanopsidae usually has been regarded as a subfamily of Thiaridae Troschel, 1857. In a cladistic analysis, Houbrick (1988) showed melanopsids to be distinct from thiarids and deserving of full familial status. In his analysis, the Melanopsidae is in a separate branch but relatively close to the branch supporting the Thiaridae.

Subfamily Melanopsinae Adams & Adams, 1854

Discussion: Houbrick (1988, 1991) confusingly assigned subfamily Melanopsinae to the family Thiaridae. Usage of this subfamily name with family Thiaridae, however, is not correct because Melanopsinae, by definition, has to be a subset of family Melanopsidae. It is in the latter sense, that the name Melanopsinae is used in this paper.

Genus *Loxotrema* Gabb, 1868

Original description: "Shell elongate, turrited, spire high; aperture with a very short canal in front; outer lip retreating above, sinuous below; inner lip heavily encrusted" (Gabb, 1868:147).

Type species: *Loxotrema turritum* Gabb, 1868, by original designation.

Loxotrema turritum Gabb, 1868
(Figures 3–14)

Loxotrema turrita Gabb, 1868:147, pl. 14, fig. 21; 1869:168, 227, pl. 28, fig. 49. Cooper, 1894:61. Cossmann, 1904: 103. Arnold, 1909:14, pl. 4, fig. 17. Arnold & Anderson, 1910:71, pl. 26, fig. 17. Arnold & Hannibal, 1913: 572. Dickerson, 1913:285; 1914:115; 1916, 439, 450 (in

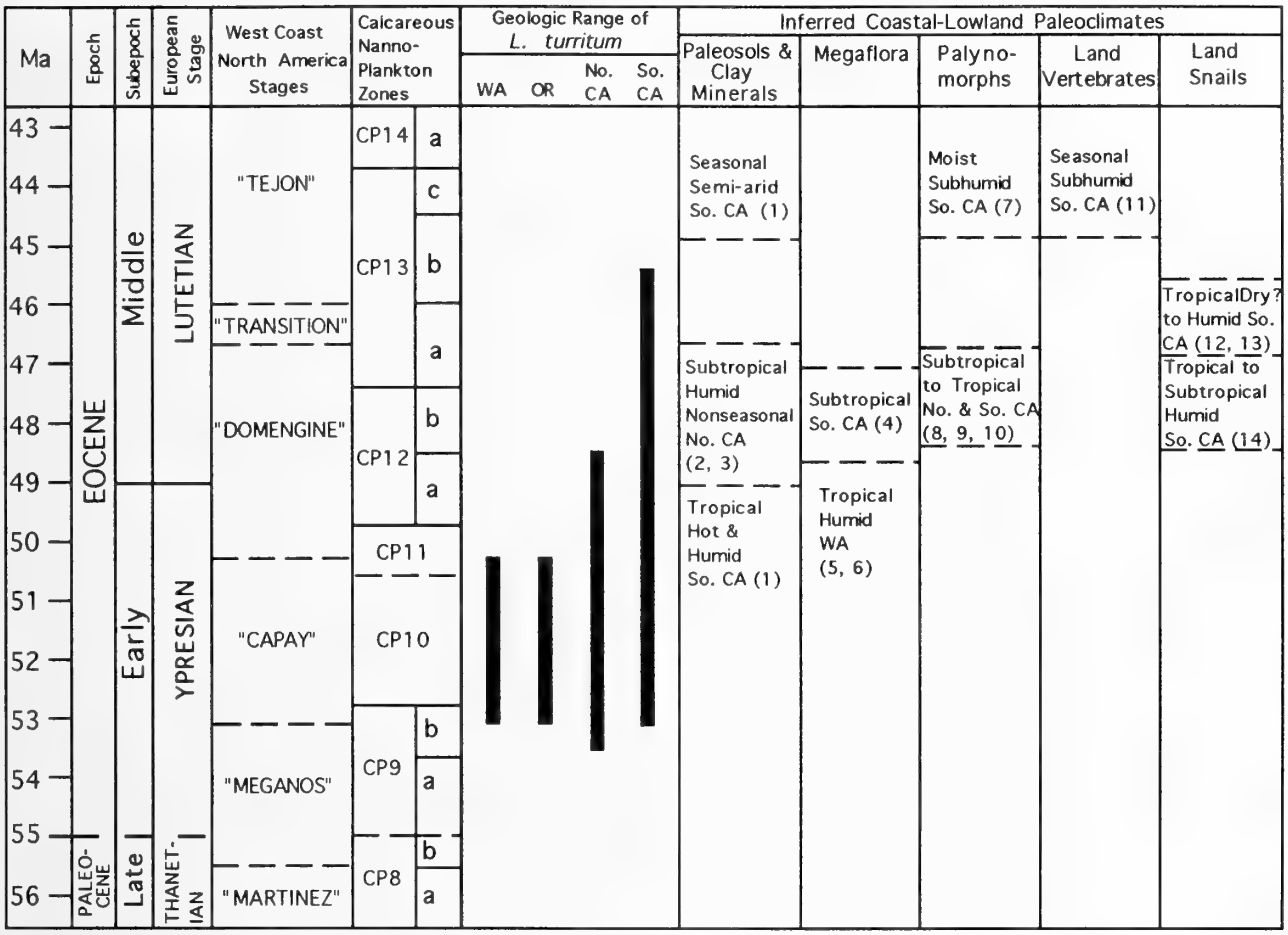

Figure 2

Geologic range of *Loxotrema turritum* Gabb, 1868, plotted against geochronologic time scale, European stages, standard calcareous nannoplankton zones (from Berggren et al., 1995), western North America stages (from Saul, 1983; Squires, 1988a), and inferred coastal-lowland paleoclimates. WA = Washington, OR = Oregon, No. CA = northern California, So. CA = southern California. Numbers in parentheses refer to the following literature sources: (1) Peterson & Abbott, 1979; (2) = Todd, 1968; (3) = Todd & Monroe, 1968; (4) = Meyers, 1991; (5) = Wolfe, 1968; (6) = Wolfe, 1994; (7) = Frederickson, 1991a; (8) = Elsik & Boyer, 1977; (9) = Lowe, 1974, quoted in Lillegraven, 1979; (10) = Schulein, 1993; (11) = Novacek & Lillegraven, 1979; (12) = Roth, 1988; (13) = Roth & Pearce, 1988; (14) = Roth, 1991.

part). Kew, 1924:29. Clark, 1926:115; 1929:pl. 10, fig. 3. Hanna, 1927:312, pl. 50, figs. 5–8. Merriam & Turner, 1937:table 2. Vokes, 1939:159, pl. 20, figs. 15–19. Schenck & Keen, 1940:pl. 24, figs. 10–13. Weaver (1942 [1943]):374, pl. 75, figs. 1–3; pl. 103, fig. 18. Keen & Bentson, 1944:168.

Struthiolaria (*Loxotrema*) *turrita* (Gabb). Tryon, 1883:196, pl. 60, fig. 95; 1885:105.

"*Loxotrema turrita*" Gabb. Anderson & Hanna, 1925:44, 104.

Struthiolaria (*Loxotrema*) *turritum* Gabb. Fischer, 1884:678.

Loxotrema turritum Gabb. Stewart, 1927:347–348, pl. 26, figs. 3, 4. Turner, 1938:tables 2, 4, & 8, p. 81, pl. 17, figs. 12, 13. Givens, 1974:70, pl. 6, fig. 17. Givens & Kennedy, 1976:963, pl. 1, figs. 5–8; 1979:table on p. 87. Squires, 1991a:355. Squires & Demere, 1991:table 1.

Pachychilus (*Loxotrema*) *turritum* (Gabb). Wenz, 1939:686, fig. 1968.

Loxotrema (no species designated). Baldwin, 1959:pl. 11, unnumbered figure. Fowkes, 1982:21, unnumbered figure.

?*Loxotrema turritum* Gabb. Squires, 1991b:table 1, pl. 1, fig. 16.

Original description: "Shell elongate, turreted, spire elevated, nearly twice the length of the aperture; whorls about six to six and a half, slightly convex on the sides, abruptly truncated and flat on the upper margin. Body whorl marked by eight or ten revolving lines on the anterior half, crossed by sinuous lines of growth; both sets of markings being very variable in distinctness in differ-


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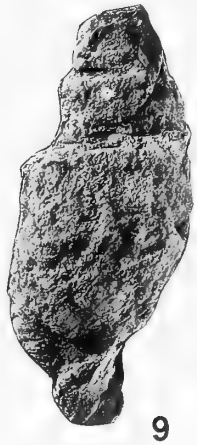
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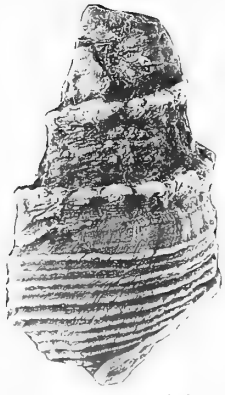
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ent specimens. Aperture obliquely subquadrate, bordered on the inner side by a raised lip, the top retreating upwards, and very obliquely backwards; outer lip thick above and below, very thin in the middle, and with a strongly sinuous margin, most prominent near the anterior end; inner lip thick, its margin somewhat raised above the surface of the body whorl; anterior extremity of aperture not notched, but produced, and slightly channelled" (Gabb, 1869:168).

Supplemental description: Medium in size (up to 45 mm high, estimated), turreted, approximately eight whorls (including protoconch); high-spired, spire about one-half of shell height; body whorl large and cylindrical. Suture in shallow groove, especially on body whorl. Protoconch approximately one whorl, low, smooth, and not well differentiated from teleoconch. Pleural angle approximately 40°. Upper spire whorls convex, remainder of teleoconch with tabulate whorls. Teleoconch sculpture changes from early whorls to later whorls. Uppermost spire whorls with two equal spiral ribs, increasing to three on middle part of spire, with posteriormost rib becoming the strongest. Spiral ribs with numerous, closely spaced small nodes; nodes strongest on posteriormost rib. Interspaces of spiral ribs with two to three very fine spiral threads forming a minute cancellate pattern with the intersecting growth lines. On lower spire and posterior part of body whorl, strength of spiral ribbing quite variable (moderately strong to smooth) and nodes obsolete except on tabulate shoulder, where nodes become very low and broadly spaced on older individuals. On anterior half of body whorl, spiral ribs strong, about eight to 20 in number; interspaces usually with a secondary spiral rib. Aperture obliquely subquadrate. Anterior end with a prominent notch. Siphonal fasciole usually weak, rarely moderately strong. Columella smooth, with a thick callus extending into parietal region and tabulate shoulder area. Posterior end of aperture (where parietal callus meets the tabulate shoulder) with a narrow notch. Outer lip sinuous, with a strong deflection medially. Outer lip projected at its anterior end and thick, thinning considerably toward the strong deflection area. Anteriormost part of outer lip crenulate, both externally and internally. Growth lines prosocline on upper spire, but opisthocline with a strong sigmoidal curve in region of the strong deflection area of the body whorl. Near suture, growth lines nearly straight to slightly opisthocline. Growth rugae commonly near outer lip on adult body whorl.

Lectotype: ANSP 4228 (designated by Stewart, 1927).

Type locality: "Tejon Group, ten miles west of Griswold's, between San Juan and New Idria" Gabb (1869:168). Vokes (1939:159) referred to topotypes of *L. turritum* from UCMP loc. A-1154, which is in the Domengine Formation, on the west side of Griswold Canyon, San Benito County, central California.

Geographic distribution: Crescent Bay, Olympic Peninsula, southwestern Washington to San Diego area, San Diego County, southern California.

Geologic age: Early Eocene ("Meganos Stage") to lower middle Eocene (lower part of "Tejon Stage").

Stratigraphic distribution: See Table 1.

Unsubstantiated stratigraphic reports: According to Anderson & Hanna (1925:104), Dickerson's (1916) report of *Loxotrema turritum* at the type section of the Tejon Formation in the southernmost part of the San Joaquin Valley, central California, is in error because there is no evidence whatsoever that it does occur there.

Turner (1938:tables 2, 8) reported *L. turritum* from the informal "lower Umpqua group" along the Middle Fork of Coquille River near Remote, southwest of Roseburg in southwestern Oregon. After a careful search, I was unable to find any of these specimens in the UCMP collection, where Turner deposited other specimens that he had collected from Eocene rocks of southwestern Oregon. Although no recent worker has assigned these reportedly *L. turritum*-bearing beds to any currently recognized stratigraphic units, the beds most likely belong to the lower Eocene undifferentiated and informal White Tail Ridge formation that has been recognized in this area by Niem et al. (1992). According to them, this formation in this area is mollusk-bearing and contains delta-front shallow-marine sandstone, as well as rare estuarine coals and mudstone. More work is needed to confirm the presence of *L. turritum* in these rocks.

←

Explanation of Figures 3 to 14

Specimens coated with ammonium chloride.
Figures 3–14. *Loxotrema turritum* Gabb, 1868. Figures 3–7. Hypotype LACMIP 6449, LACMIP loc. 7206, height 37.3 mm, ×1.8. Figure 3. Apertural view. Figure 4. Right-lateral view. Figure 5. Left-lateral view. Figure 6. Abapertural view. Figure 7. Oblique anterior view. Figure 8. Hypotype LACMIP 6450, LACMIP loc. 7206, right-lateral view, height 34.6 mm, ×1.8. Figures 9–10. Hypotype LACMIP 7162, CSUN loc. 1450, height 28 mm, ×1.9. Figure 9. Left-lateral view. Figure 10. Abapertural view. Figure 11. Hypotype LACMIP 6451, LACMIP loc. 24258, abapertural view, height 20.2 mm, ×2.5. Figure 12. Hypotype UCMP 154003, UCMP loc. A-1550, apertural view, height 21.5 mm, ×2.9. Figures 13, 14. Hypotype LACMIP 6452, LACMIP loc. 7206, apertural view. Figure 13. Height 21.2 mm, ×2.6. Figure 14. Protoconch (some shell missing) and uppermost teleoconch, height 3.5 mm, ×12.

Published reports of *L. turritum* in the Llajas Formation of Simi Valley, Ventura County, southern California are unsubstantiated because of indefinite geologic and geographic information. Kew (1924:29) listed *L. turritum* as one of the mollusks from a locality (UCMP loc. 3311) on the south side of Simi Valley. Using the locality information given by Kew, the locality does not plot in bedrock, rather it plots in the streambed of the modern Simi Arroyo. Information in the UCMP locality records is even less informative, with the locality cited only as Simi Valley. Clark (1921:155) was the original collector of the mollusks from this locality, but he did not include any details as to its location. He listed nearly the same mollusks from this locality that Kew did, but, for some reason, Clark did not include *L. turritum.* I was able to find a specimen of *L. turritum* from UCMP loc. 3311 in the UCMP collection, but the associated mollusks were totally different from those listed by Clark (1921) and Kew (1924) and are ones normally found in the shallow-marine part of the Llajas Formation that crops out on both the north and south sides of Simi Valley. This formation, which was named many years after the work of Clark (1921) and Kew (1924), is an obvious candidate for the stratigraphic position of UCMP loc. 3311. Turner (1938: table 8) even reported, by means of a checklist, that *L. turritum* is present in the "lower Llajas Formation," but he did not provide any other stratigraphic or geographic details. In my monographic study (Squires, 1984) of the megafossils of the Llajas Formation, I found no *L. turritum* anywhere in the formation. I also did a careful search at LACMIP, which has an extensive collection from the Llajas Formation, without finding any specimens of *L. turritum.* I did find several other specimens of *L. turritum* from the Llajas Formation in the collections at UCMP, CAS, and UCR, but the locality data are very indefinite.

Discussion: A total of 297 specimens of *L. turritum* was studied. Most are worn, and the upper spire sculpture usually has been nearly obliterated. The anterior notch and siphonal fasciole are best developed on adult specimens, but even these show variability as to strength of the siphonal fasciole. A weak siphonal fasciole is illustrated in Figure 5, whereas a much stronger one is illustrated in Figures 9 and 10.

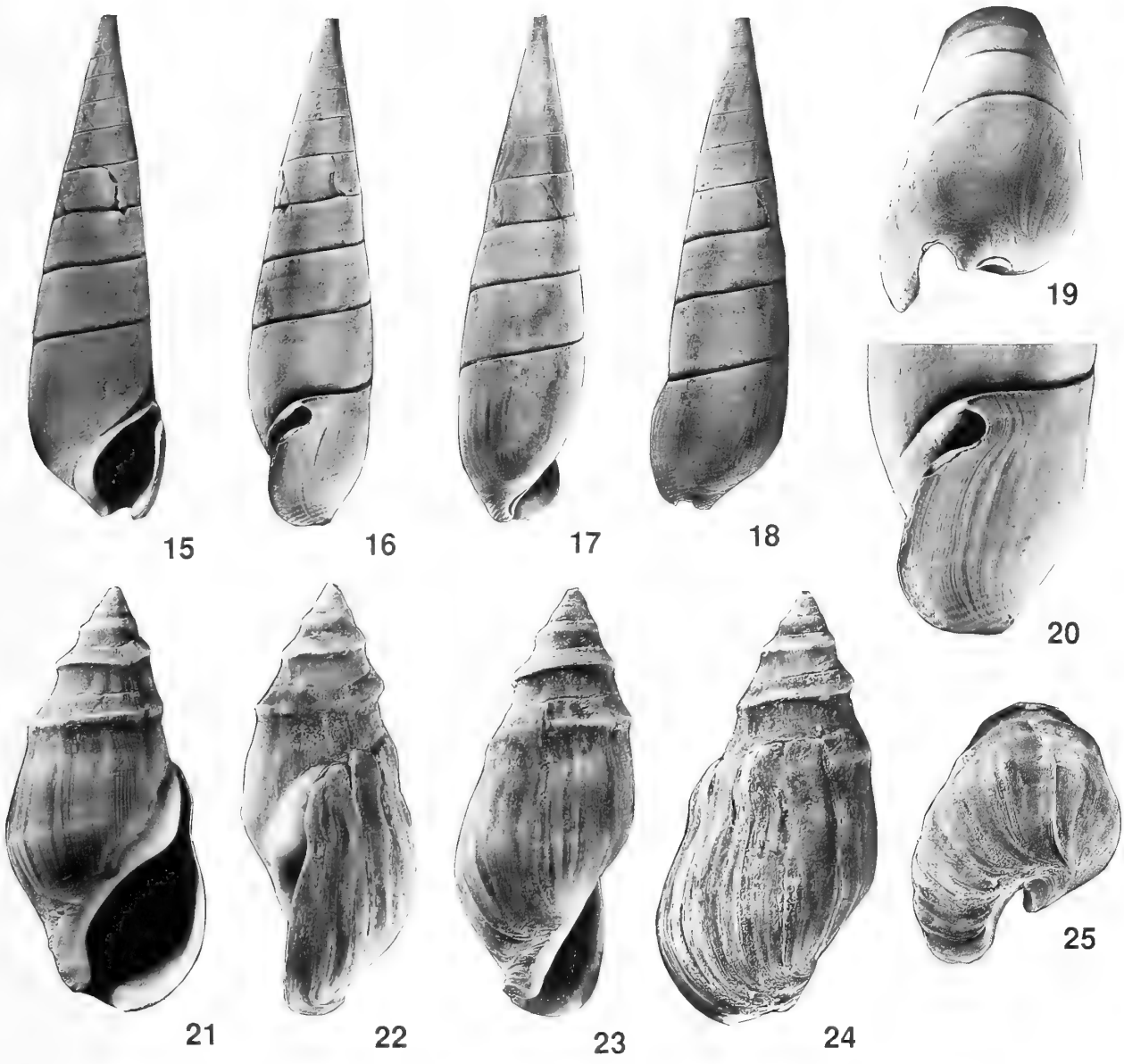
The most numerous specimens were found in the Crescent Formation at Crescent Bay, Washington. Nearly all of these are early adults and show very well the sculpture on the upper spire. One of these specimens is illustrated in Figure 12. Some specimens from the upper part of the Matilija Sandstone at Matilija Hot Springs show nodes on the shoulder of the adult body whorl. One of these specimens is illustrated in Figure 11.

In terms of the apertural notches and outline of the outer lip, *L. turritum* most closely resembles *Faunus ater* Linnaeus, 1758, the type species and only living species of *Faunus.* Houbrick (1991:figs. 1–18) reported *F. ater* from freshwater to slightly brackish-marine habitats in the Indo-West Pacific. Utilizing LACM specimens (lot number 107993) for comparison, both genera have a subquadrate apertural shape, a well-developed anterior notch, a posterior notch, a projected anterior end of the aperture, a sinuous outer lip, and a siphonal fasciole. A specimen of *F. ater* is illustrated in Figures 15–20. The aperture of *Loxtrema* differs only in minor ways by having shallower anterior and posterior notches, a much narrower posterior notch, usually a weaker siphonal fasciole, and a crenulated anterior end of the outer lip. In terms of the rest of the shell, *Loxotrema* differs by having a much lower spire, tabulate whorls, presence of shell sculpture, no subsutural band on the adult body whorl, and deflection of the outer lip-area ophisthocline growth lines nearer the suture.

After a detailed anatomical study of *F. ater,* Houbrick (1991) assigned *Faunus* to subfamily Melanopsinae and reported that *F. ater* has certain unusual anatomical features that unite *Faunus* to the melanopsid *Melanopsis* and to the thiarid *Melanatria* Bowdich, 1822. Houbrick (1991) also discussed how the classification of *Faunus* is still very provisional and that much work is needed to clarify its exact phylogenetic relationship with the thirarid group, a large and poorly defined family of freshwater prosobranchs in need of major revision.

Loxotrema turritum closely resembles the living species *Melanopsis* (*Lyrcaea*) *dufouri* Férussac, 1823, the type species of *Lyracea. Melanopsis* (*L.*) *dufouri* was illustrated by Wenz (1939:691, fig. 1987), who reported it from Valencia, Spain. Subgenus *Lyrcaea* is generally smoothish, ranges from Eocene to Recent, and its fossil record is in Europe, North Africa, and Asia. Today it is confined to the Mediterranean region (Wenz, 1939). Comparison with LACM specimens (lot number 108173) of *M.* (*L.*) *dufouri,* from a floodplain-river system near Sevilla, Spain, revealed that *Loxotrema turritum* differs from this species by having a higher spire, shorter body whorl, spiral ribbing on the whorls rather than just a swollen spiral rib at the whorl shoulder, an oblique posterior notch rather than a vertical one, usually a much weaker siphonal fasciole, and a more sigmoidal growth line on the body whorl. A specimen of *M.* (*L.*) *dufouri* is illustrated in Figures 21–25.

Loxotrema turritum is also somewhat similar to *Cerithium*? *macarum* Olsson (1931:183–184, pl. 28, fig. 3) in terms of general shape, upper spire ornamentation, and growth-line shape on the body whorl. *Cerithium*? *macarum,* which has been found in the Oligocene Mancora Formation of Peru, is known from only a single specimen, and it lacks the aperture and the tip of the spire. *Loxotrema turritum* differs from this species by having a longer body whorl, much shorter spire, more inflated body whorl, more prominent spiral ribs on body whorl, more tabulate and nodose shoulder on the whorls, and no in-



Explanation of Figures 15–25

Specimens coated with ammonium chloride.

Figures 15–20. *Faunus ater* Linnaeus, 1758, hypotype LACM 107993, Recent, Sri Lanka (Ceylon), height 63 mm, ×1.2 Figure 15. Apertural view. Figure 16. Right-lateral view. Figure 17. Left-lateral view. Figure 18. Abapertural view. Figure 19. Oblique anterior view. Figure 20. Enlarged right-lateral view of body whorl. Figures 21–25. *Melanopsis* (*Lyrcaea*) *dufouri* Férussac, 1823, hypotype LACM 108173, Recent, Sevilla, Spain, height 25.4 mm, ×2.4. Figure 21. Apertural view. Figure 22. Right-lateral view. Figure 23. Left-lateral view. Figure 24. Abapertural view. Figure 25. Oblique anterior view.

dication of varices. Until better material is found for Olsson's species, its generic assignment is open to question.

Loxotrema turritum generally resembles the living species *Aylacostoma glabrum* Spix, 1827 (in Spix & Wagner, 1827), which is the type species of *Aylacostoma*. *Aylacostoma glabrum* was recently described and illustrated by Nuttall (1990:259, 261, figs. 286–291), who reported it from a freshwater habitat in eastern Brazil. This genus belongs to family Thiaridae and subfamily Hemisininae Thiele, 1928. The only other known species of this genus is *Aylacostoma* sp., which is based on poorly preserved specimens of Miocene age from Ecuador (Nuttall, 1990). *Aylacostoma glabrum* shows considerable variation in morphology. It can be smooth or have rather strong sculp-

ture, and the body whorl can be almost straight-sided or strongly shouldered with a marked ramp. All of these variants are well illustrated by Nuttall (1990). *Loxotrema turritum* resembles only those specimens of *A. glabrum* that are smoothish and strongly shouldered (see Nuttall, 1990:figs. 286–287) and differs significantly from them by having a posterior notch in the aperture, a protruding (hoodlike) anterior portion of the outer lip rather than a slight concavity there, a weak siphonal fasciole, a sigmoidal growth line rather than a slightly sinuate one, shorter spire, tabulate spire whorls, beaded upper spire whorls, and a projecting and much thicker callus along the inner lip. In addition, *L. turritum* does not have a ramp associated with its strongly tabulate body whorl shoulder. In spite of the many differences between these two taxa, their overall similarilty does suggest a case of convergence.

Loxotrema turritum is only the second melanopsid recognized in the fossil record of the Pacific slope of North America. The other one is *Boggsia tenuis* (Gabb, 1864), known from the Upper Cretaceous (Campanian Stage) strata in northern California (Squires & Saul, 1997).

The name *Loxotrema* is a combination of *loxos* (Greek, slanting or crosswise) and the neuter noun *trema* (Greek, hole). Although early workers used the name "*turrita,*" Fischer (1884) was correct in using the name "*turritum*" because *turritus* (Latin, with towers or castellated) is an adjective and its ending has to agree in gender with the genus.

STRATIGRAPHIC DISTRIBUTION AND DEPOSITIONAL ENVIRONMENTS

Introduction

Loxotrema turritum is known from numerous areas in California, two areas in Oregon, and one area in Washington (Figure 1). Its geologic range for each of these states is depicted in Figure 2. The formations in which it is found, as well as the associated inferred depositional environments, are given in Table 1.

"Meganos Stage"

The only known "Meganos Stage" record of *L. turritum* is new information. It is also the earliest record of this species, which was reported formerly by various workers (Table 1) to be no earlier than the "Capay Stage." The "Meganos Stage" record is based on a single worn specimen from a sandstone (UCMP loc. 3586) in the Kellogg Creek area of Contra Costa County in northern California. This sandstone was referred to as "division D of the Meganos Formation" by Clark & Woodford (1927), but modern workers use the name "Margaret Hamilton Sand" (Edmondson, 1984). Division D of the Meganos Formation is correlative with the middle of the CP9 Zone of the standard calcareous nannoplankton zonation (Almgren et al., 1988). This part of the CP9 Zone is correlative with the "Meganos Stage" (Squires, 1988a). Almgren (1978) reported the Margaret Hamilton Sand to contain benthic foraminifera indicative of a probable mid-neritic (shallow marine) environment of deposition. The mollusks found associated with *L. turritum* at UCMP loc. 3586 (Clark & Woodford, 1927:82–84) also indicate a shallow-marine environment. The broken and worn condition of the *L. turritum* specimen indicates that it was probably transported to the site.

"Capay Stage"

Only a single CSUN collection specimen was found in the "Capay Stage" Maniobra Formation of the Orocopia Mountains of Riverside County in southern California. This specimen, which is poorly preserved and worn, was tentatively identified (Squires, 1991b:pl. 1, fig. 16, table 1) as *L. turritum.* I now consider it to be *L. turritum.* This specimen is part of a relatively diverse and mostly shallow-marine megafossil assemblage that was interpreted as having lived in nearshore waters adjacent to a submarine canyon and was transported basinward into the bathyal depths of the submarine canyon (Advocate et al., 1988; Squires, 1991b).

Merriam & Turner (1937:table 2) reported *L. turritum* as part of a moderately diverse and mostly shallow-marine megafossil assemblage from the Capay Formation at the type section of the formation as Smith Canyon, Yolo County, northern California. I examined the UCMP collection specimens and found them to be poorly preserved. Redwine (1984) reported that the lower Eocene Capay Formation represents displaced material derived mostly from nearshore depths and deposited as turbidites in the lower part of the Princeton Submarine Valley system, whose length was approximately 265 km. These *L. turritum* specimens, therefore, probably underwent considerable postmortem transport.

The "Capay Stage" specimens of *L. turritum* from Crescent Bay, Washington (UCMP locs. A-1547, A-1550) represent a new occurrence and extend, a distance of 580 km, this species' northernmost record, which was previously reported to be in southwestern Oregon (Turner, 1938). These Washington specimens differ from other "Capay Stage" specimens by having lived in coastal waters on the flank of a basalt volcano. These abundant and well-preserved UCMP collection specimens, all about 22 mm high and showing the delicate upper spire sculpture, were found in sedimentary interbeds in basalt flows of the Crescent Formation on the west side of Crescent Bay, Clallam County, Olympic Peninsula, southwestern Washington. Duncan (1982) proposed that this Crescent Formation basalt formed oceanic seamounts that became accreted, by means of subduction-zone tectonics, to the margin of the North American continent. More recently, Babcock et al. (1992) proposed that the basalt formed

Table 1

Formations containing *Loxotrema turritum* and their inferred depositional environments. Stages listed youngest to oldest, in descending order. [CA = California, OR = Oregon, WA = Washington, * = New occurrence].

Formation; location; literature sources	Inferred depositional environment; literature sources
"TEJON STAGE":	
Matilija Sandstone, Pine Mtn., Ventura Co., CA (Givens, 1974)	Mixed brackish-marine bays or lagoons & shallow marine at the seaward margin of a delta complex (Givens, 1974)
Matilija Sandstone, mouth of Alamo Creek, Ventura Co., CA (Givens, 1974)	Brackish-marine bays or lagoons on a delta complex (Givens, 1974)
Juncal Formation (sandstone facies), Pine Mtn., Ventura Co., CA (Givens, 1974)	Mixed brackish-marine bays or lagoons & shallow marine (beach & bar) at the seaward margin of a delta complex (Givens, 1974)
Matilija Sandstone, Beartrap Creek, Ventura Co., CA (Squires, 1991a)	Mixed brackish marine & nearshore marine (Squires, 1991a)
"TRANSITION STAGE":	
Matilija Sandstone, Matilija Hot Springs, Ventura Co., CA (Squires, 1991a)	Brackish-marine lagoon or bay in close association with beach-bar-barrier complexes (Link, 1975; Link & Welton, 1982; Squires, 1991a)
Juncal Formation (siltstone facies), NE of Pine Mtn., Ventura Co., CA (Givens, 1974)	Interdistributary bays or lagoons or prodelta at the seaward margin of a delta complex (Givens, 1974)
Scripps Formation, Murphy Canyon, San Diego Co, CA (Squires & Demere, 1991)	Nearshore shallow-marine with some transported brackish-marine lagoonal mollusks (Squires & Demere, 1991)
"DOMENGINE STAGE":	
*Ardath Shale, Blacks Canyon, San Diego Co., CA	Bathyal (600 to 1500 m depth) submarine-fan channel fill with reworked shallow-marine fossils (Lohmar et al., 1979; May & Warme, 1991)
Delmar Formation, Torrey Pines State Reserve, San Diego Co., CA (Hanna, 1927; Givens & Kennedy, 1979)	Marginal-marine oyster bioherms in a bay, estuary, or lagoon (Hanna, 1926; Lohmar et al., 1979; Warme, 1991; May & Warme, 1991)
Santiago Formation, Vista, Sand Diego Co., CA (Givens & Kennedy, 1976)	Marine or brackish marine, perhaps lagoon or estuary (Givens & Kennedy, 1976)
Domengine Formation, Vallecitos syncline, San Benito Co., CA (Vokes, 1939; Schulein, 1993)	Brackish-marine lagoon on a deltaic complex (Schulein, 1993)
Domengine Formation, Coalmine Canyon, Fresno Co., CA (Arnold, 1909; Arnold & Anderson, 1910; Vokes, 1939)	Swampy intertidal distributary bay on a delta complex (Roush, 1986)
"CAPAY STAGE"	
White Tail Ridge formation, Glide, Douglas Co., OR (Turner, 1938)	Mixed fluvial & shallow marine on a delta complex (Niem et al., 1992)
*Crescent Formation, Crescent Bay, Clallam Co., WA	Rift-zone? volcanic island in marine waters (Babcock et al., 1992)
Maniobra Formation, Orocopia Mtns., Riverside Co., CA (Squires, 1991b)	Bathyal submarine-canyon fill, very near a coastline (Advocate et al., 1988; Squires, 1991b).
Capay Formation, Smith Canyon, Yolo Co., CA (Merriam & Turner, 1937)	Bathyal (760 to 1830 m depth) submarine-valley fill (Redwine, 1984)
"MEGANOS STAGE"	
*Margaret Hamilton Sand, Kellogg Creek, Contra Costa Co., CA	Probable mid-neritic (shallow marine) (Almgren, 1978)

volcanic islands within a rift zone along the margin of the continent, and this tectonic setting seems much more likely for *L. turritum* than one associated with oceanic seamounts. At UCMP loc. A-1547, *L. turritum* was found associated with a diverse shallow-marine, mega-invertebrate assemblage consisting of many species of mollusks and a species of colonial coral. Many of these same species of mollusks were reported by Arnold & Hannibal (1913:572) from the Crescent Formation near Tongue Point on the east side of Crescent Bay. At UCMP loc. A-1550, *L. turritum* was found associated with shallow-marine mollusks and some specimens of the gastropod *Potamides* (*Potamides*?) *carbonicola* Cooper, 1894. This potamidid has been reported by many workers (e.g., Arnold, 1909) as diagnostic of brackish-marine environments. The presence of it in the Crescent Formation is new information. Elsewhere in southwestern Washington, the upper part of the Crescent Formation has yielded mollusks and other megafossils that lived on the hard substrate formed where extrusion of basalt caused shoaling

of marine waters. The megafaunas were subject to storm waves and were transported down steep slopes into shallow, subtidal depths where other mollusks lived (Squires et al., 1992; Squires & Goedert, 1994a, b, 1995, 1996). In all these previously studied areas, however, *L. turritum* has not been found, but at one locality in the Crescent Formation at Larch Mountain, Black Hills near Olympia, Squires & Goedert (1994a) reported the presence of the ellobiid *Ovatella* (*Myosotella*), a pulmonate (air-breathing) gastropod indicative of salt marshes and upper shores or estuaries. Evidently, the early Eocene volcanic island in the Crescent Bay region was associated with localized brackish-marine environments. The uniform size of the *L. turritum* specimens indicates sorting associated with postmortem transport, but the presence of delicate upper spire sculpture on these specimens indicates that the distance of transport was not great. Detailed paleo-environmental studies of the Crescent Formation in the Crescent Bay area are much needed.

The taphonomy of the specimens of *L. turritum* from the Maniobra, Capay, and Crescent formations is similar to that reported (Givens, 1994; Squires & Advocate, 1986; Squires, 1997) for some other early Eocene gastropods that lived in coastal waters along the tectonically active coast of California. Like *L. turritum,* they were subject to transport into deeper waters via turbidity currents.

Turner (1938) reported specimens of *L. turritum* in the Glide area of southwestern Oregon. The specimens are from the informal White Tail Ridge formation (A. Niem, personal communication, 1996), which is correlative to the upper Umpqua formation or the Lookingglass Formation, both of previous usage (Niem et al., 1992). The White Tail Ridge formation is assignable to the lower Eocene calcareous nannofossil CP11 Zone, which ranges from the upper part of the "Capay Stage" to the lower part of the "Domengine Stage" (Squires, 1988a). Givens & Kennedy (1976) believed that the rock unit at Glide might possibly be assignable to the "Domengine Stage," but the presence of *Turritella andersoni* Dickerson, 1916, a species diagnostic of the "Capay Stage" (Squires, 1988b), indicates that the rock unit is assignable to the "Capay Stage." It is likely that the Glide specimens are in rocks correlative to near the boundary between the "Capay Stage" and the "Domengine Stage." Although the White Tail Ridge formation consists of deltaic (mixed fluvial and shallow-marine) deposits (Niem et al., 1992), the actual beds containing the specimens of *L. turritum* have not been incorporated by any recent worker into a detailed depositional-model context. Several years ago, before I began this present investigation, I collected specimens of *L. turritum* from this formation in the Glide area at UCMP locs. A-661 and A-662. The specimens are in sandy lenses of transported fossils, and the lenses are about 15 to 20 m in lateral extent. The richest lens is at locality A-661, which is about 5 m stratigraphically below the lens at locality A-662. At locality A-661, there are abundant specimens of *L. turritum,* ranging in height from 17 to 40 mm (estimated). Many of them are nearly complete and are missing only the protoconch, the anterior end of the aperture, and the outer lip. The upper spire sculpture has been somewhat abraded, and although the specimens have undergone some postmortem transport they were not transported very far. Overall, the shells at this locality show better preservation than at any other locality where *L. turritum* has been found. There are also a few specimens of *Potamides* (*P.*?) *carbonicola* present at locality A-661.

"Domengine Stage"

Arnold (1909) and Arnold & Anderson (1910) reported *L. turritum* from a section of middle Eocene rocks containing lignite and gypsiferous sandstone at Coalmine Canyon about 7 km northwest of Coalinga, central California, and they interpreted that these rocks were brackish marine. These rocks are now referred to as the Domengine Formation (Vokes, 1939:20). Roush (1986:81, figs. 5B, 25) studied the details of the depositional environment of the Domengine Formation at Coalmine Canyon, and although she found no *L. turritum,* she interpreted that the beds accumulated in an interdistributary bay on a river-dominated delta associated with a low-energy coastline where swamps were present.

Vokes (1939) reported *L. turritum* from the Domengine Formation in the Vallecitos syncline area between New Idria and Panoche, about 50 km north of Coalinga. In addition, he confirmed the presence of this species in the Domengine Formation at Coalmine Canyon. Vokes (1939:159) reported, furthermore, that *L. turritum* is a brackish-marine species and is always associated with *Acutostrea idriaensis idriaensis* (Gabb, 1869) and *Potamides* (*P.*?) *carbonicola.* He did not make it clear if he was referring to only the Vallecitos syncline area or to everywhere *L. turritum* is present. *Loxotrema turritum* is not always associated with these two species. Schulein (1993) studied the details of the depositional environment of the Domengine Formation in the Vallecitos syncline area. In the Griswold Canyon area in the central part of this syncline, he found *L. turritum,* usually associated with *P.* (*P.*?) *carbonicola* and *A. idriaensis idriaensis,* in lenses interbedded with carbonaceous claystone and siltstone. He interpreted the formation in this particular area as having been deposited on a deltaic complex and that these species represent nearly *in situ* brackish-marine lagoonal assemblages, or that they had undergone slight postmortem transport and accumulated at the seaward edge of a salt marsh.

Givens & Kennedy (1976) reported *L. turritum* from a small molluscan assemblage in middle Eocene ("Domengine Stage") strata near Vista in northern San Diego County, southern California. Although none of the spec-

imens of this species is complete, they show good preservation and their depositional environment was interpreted (Givens & Kennedy, 1976) as having been "a low-energy, very shallow (0–30 m) marine or brackish-water environment, perhaps in a lagoon or estuary." These rocks are now assigned to the Santiago Formation (Eisenberg & Abbott, 1991).

Hanna (1926) reported *L. turritum* from the Delmar Formation near San Diego, and he interpreted the formation to be a brackish-marine deposit. Many sedimentological studies in recent years (e.g., Kennedy & Moore, 1971; Lohmar et al., 1979; Warme, 1991; May & Warme, 1991) have supported the interpretation that the Delmar Formation was deposited in a stream-mouth lagoonal setting.

The presence of rare reworked specimens of *L. turritum* in the Ardath Shale at Blacks Canyon, San Diego County, southern California, represents the only post-"Capay Stage" record of this species in deep-marine rocks. This occurrence is new information. The specimens, which are from the upper 4 m of the Ardath Shale at UCR loc. 4930, have their apertures filled with clean, medium-grained sand matrix that is distinctly different from the surrounding siltstone, thereby indicating that the shells were transported prior to burial. The Ardath Shale consists of canyon fill deposited at depths between 600 and 1500 m. The submarine canyon incised into older shallow-water deposits of the Delmar Formation and other formations (Lohmar et al., 1979; May & Warme, 1991), and the Delmar Formation was most likely the source for the specimens of *L. turritum.*

"Transition Stage"

Roth (1988) and Squires & Demere (1991) reported *L. turritum* from SDSNH loc. 3278 in the Friars Formation at Murphy Canyon in the San Diego area. Walsh et al. (1996), however, reassigned the rocks at this locality to the laterally interfingering and subjacent upper part of the Scripps Formation. The *L. turritum* at this locality represents part of a transported and rare, but distinct, brackish-marine element of an otherwise moderately diverse nearshore, shallow-marine molluscan assemblage (Roth, 1988; Squires & Demere, 1991).

Givens (1974:table 1) reported *L. turritum,* along with *Potamides* (*P.*?) *carbonicola* and *Acutostrea idriaensis idriaensis,* at a single locality (UCR loc. 4696) in the *Ectinochilus supraplicatus* megafaunal biozone in the siltstone facies of the Juncal Formation about 2.5 km northeast of Pine Mountain, Ventura County, southern California. He also interpreted that the siltstone facies might have been deposited in interdistributary bays or lagoons or in the prodelta environment of the seaward edge of the deltaic complex.

The middle Eocene upper part of the Matilija Sandstone at Matilija Hot Springs in Ventura County, southern California contains numerous specimens of *L. turritum* within a 50 m-thick section of alternating sandstone and finer grained intervals consisting of complexly interbedded mudstone, fossiliferous mudstone, siltstone, and, in some cases, gypsum and limestone. Link (1975) and Link & Welton (1982) reported the section represents a restricted-coastal (paralic) environment, with three main subenvironments: beach-bar-channel complexes [= sandstone], lagoon or bay [= mudstone, fossiliferous mudstone, and siltstone], and coastal sabkha [= gypsum, limestone, mudcracks, and localized "red beds"]. Based on my own fieldwork, which is being incorporated into a detailed report of the molluscan fauna of these restricted-coastal rocks (Squires, in preparation), I found that *L. turritum* is present in several thin, silty mudstone beds immediately overlain by unfossiliferous mudstone or siltstone. Common associates are the gastropod *Potamides* (*Potamidopsis*) *californica* Squires, 1991a, the oyster *Acutostrea idriaensis idriaensis,* and corbiculid, tellinid, and venerid bivalves. The specimens of *L. turritum* and *P.* (*P.*) *californica* range in size from early juveniles to adults, show delicate sculpture, are mostly complete, and are randomly oriented. Many of the bivalve specimens are closed-valved. The distance of postmortem transport of any of these mollusks has been small, and the specimens have not been moved out of their original habitat. They represent nearly *in situ* brackish-marine individuals that lived in restricted-coastal waters. Some of the fossiliferous mudstones in this section contain lenses of gypsum and/or limestone. In comparison with the other fossiliferous mudstones, these mudstones directly associated with evaporites have a much lower taxonomic diversity of mollusks. Although *Potamides* (*Potamidopsis*) *californica* persists as a common faunal component in these mudstones associated with evaporites, *L. turritum* is never present, and its absence indicates that it did not tolerate evaporitic conditions.

"Tejon Stage"

Jestes (1963) and Squires (1991a) reported a storm-derived mixture of nearshore-marine and brackish-marine mollusks, including *L. turritum,* in the Matilija Sandstone in the vicinity of Beartrap Creek, just east of the mouth of Alamo Creek, Ventura County, southern California. Givens (1974) assigned the rocks in this part of the Matilija Sandstone to the "Tejon Stage."

Givens (1974:table 1) reported *L. turritum* from the *Ectinochilus canalifer* megafaunal biozone in the sandstone facies of the Juncal Formation just north of Pine Mountain, Ventura County, southern California. Some mollusks in this facies are indicative of the shallow-marine environment, possibly at the seaward margin of a delta complex, whereas others (oyster banks and *Potamides* (*P.*?) *carbonicola*) are indicative of brackish-water bays or lagoons (Givens, 1974).

Givens (1974:table 1) also reported *L. turritum* from the *Ectinochilus canalifer* biozone in the lower part of the Matilija Sandstone at the mouth of Alamo Creek, Ventura County, southern California. Associated mollusks (e.g., *Potamides* (*P.*?) *carbonicola* and *Acutostrea idriaensis idriaensis*) indicate that these rocks were probably deposited in brackish-water bays or lagoons (Givens, 1974).

Givens (1974:table 1), furthermore, reported a mixture of shallow-marine and brackish-marine mollusks, including *L. turritum,* in the *Ectinochilus canalifer* biozone in the Matilija Sandstone just east of Pine Mountain, Ventura County, southern California, and he interpreted the depositional environment of these mollusks to have been probably adjacent to a delta complex.

PALEOCLIMATE

Introduction

Inferred paleoclimatic conditions for the geologic range of *L. turritum* are summarized in Figure 2. Eocene rocks in San Diego County, southern California, are particularly useful for paleoclimate studies because of the complex intertonguing relationships between shallow-marine and nonmarine formations. These stratigraphic relationships span nearly the entire Eocene, and many types of geologic studies have been done on these rocks.

"Meganos Stage" and "Capay Stage"

Loxotrema turritum was most widespread (from Washington to southern California) during the time of the "Meganos Stage" and the "Capay Stage." This early Eocene time was the warmest interval of the Cenozoic, and tropical to subtropical conditions were widespread (Haq, 1981). On the west coast during this time, tropical and hot-humid conditions prevailed in coastal-lowland areas, as revealed by studies of a lateritic paleosol and of megafloral fossils (Figure 2). The paleosol study was done in the San Diego area, southern California, and in northwestern Baja California, Mexico (Peterson & Abbott, 1979). The megafloral study was done on the lower Eocene part of the Puget Group of southwestern Washington (Wolfe, 1968; 1994).

"Domengine Stage"

The "Domengine Stage" record of *L. turritum* is known only from California. From the middle part of this stage (lowermost middle Eocene) through the end of the geologic range of this species in the lower part of the "Tejon Stage" (lower middle Eocene), *L. turritum* is known only from southern California. During this same interval, tropical to subtropical conditions were prevalent in coastal-lowland areas, as revealed by studies of clay mineralogy, megafloral fossils, palynomorphs, and land snails (Figure 2). The clay mineralogy study was done on the Domengine Formation in northern California (Todd, 1968; Todd & Monroe, 1968), and the megafloral studies were done on the Torrey Sandstone in the San Diego area (Myers, 1991). This latter formation has been reported by many workers (e.g., May & Warme, 1991) as interdigitating laterally with both the marine Ardath Shale and the brackish-marine Delmar Formation. Palynomorph studies were done on the Ardath Shale (Lowe, 1974; quoted in Lillegraven, 1979), on the Delmar Formation (Elsik & Boyer, 1977), and on the Domengine Formation in the Vallecitos syncline area in northern California (Schulein, 1993). A land snail was studied from the Santiago Formation at Oceanside in northern San Diego County (Roth, 1991).

"Transition Stage"

The Scripps Formation record of *L. turritum* at Murphy Canyon (SDSNH loc. 3278) in the San Diego area is also associated with land snails. A study of camaenid land snails from the upper part of this formation indicated "forested land and a tropical climate with ample summer rainfall," and the land snails might have been living in a humid forest fringing a coastal lagoon (Roth, 1988). A single specimen of a transported helicinid land snail from elsewhere in the Scripps Formation could indicate tropical conditions, but paleoclimate inferences based on helicinids are somewhat inconclusive because modern members of this family range into xeric (dry) habitats (Roth & Pearce, 1988).

Lower Part of the "Tejon Stage"

In the San Diego area, the Scripps Formation laterally interfingers with and is partly subjacent to the chiefly nonmarine Friars Formation. Just upsection from the Friars Formation is the marine to nonmarine Mission Valley Formation. Neither of these two formations contains specimens of *L. turritum,* but both (especially the Mission Valley Formation) record a climatic change to less humid conditions (Peterson & Abbott, 1979). The Mission Valley Formation is correlative in time to just after the disappearance of *L. turritum* from the rock record. Frederickson (1991b) assigned this formation to the calcareous nannoplankton Subzone CP13c, but Walsh et al. (1996) suggested that it might be assignable to the slightly younger Subzone CP14a (equivalent to the lower part of the "Tejon Stage"). Caliche horizons, immature clay-mineral suites, and apparent salt crystallization from the Friars and Mission Valley formations have led to the conclusion that the paleoclimate during the deposition of these rock units was distinctly seasonal and arid (Peterson & Abbott, 1979). A study of over 100 species of land vertebrates from these same formations have led to the conclusion that the paleoclimate was seasonal and dry to moist subhumid (Novacek & Lillegraven, 1979). Frederickson (1991a) reported that the angiosperm-pollen flora from near the base of the Mission Valley Formation indicates

that the climate was seasonal and no dryer than moist subhumid.

The synchronism between the disappearance of *Loxotrema turritum* and the change of climate from subtropical/tropical to seasonal semiarid strongly suggests that the extinction of this species was caused by climatic change. The species was adapted for humid, tropical conditions as evidenced by its widespread dispersal during the early Eocene. It is important to mention that the environment of *Faunus ater,* which is the closest living relative of *Loxotrema turritum,* is also confined to fully tropical conditions. *Faunus ater* is found today in the mouths and coastal reaches of freshwater rivers and streams, where there is some brackish influence, between 20°N and 20°S of the equator in southeast Asia, Sumatra, Java, Moluccas, Thailand, Sri Lanka (Ceylon), China, Philippines, New Guinea, Solomon Islands, and New Hebrides (Houbrick, 1991).

The presence of *L. turritum* in nearly *in situ* conditions in the upper part of the Matilija Sandstone at Matilija Hot Springs is especially revealing. As discussed earlier, it is present in fossiliferous mudstones not directly associated with evaporites, but it is always absent in fossiliferous mudstones containing lenses of evaporites. Although *Loxotrema turritum* was rather hardy because it lived in the brackish-marine environment, it could not tolerate arid conditions, and it is very likely that when the climate became too dry during the early middle Eocene the species went extinct.

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LOCALITIES CITED

CSUN 1450. About 225 m (836 ft.) W of junction of Highway 33 and a short, paved road that leads to Matilija Hot Springs, on S bank of North Fork Matilija Creek near W end of highway bridge that crosses the creek, NE ¼ of the SE ¼ of section 29, T. 5 N, R. 23 W, U.S. Geological Survey Matilija Quadrangle, 7.5-minute, 1952 (photorevised 1967), Ventura County, southern California. Matilija Sandstone. Age: Early middle Eocene ("Transition Stage"). Collector: R. L. Squires, 1990 and 1996.

LACMIP 7206. On E bank of Little River just S of highway bridge over the river at Glide, SE ¼ of the NW 14 of section 19, T. 26 S, R. 3 W, U.S. Geological Survey Glide Quadrangle, 15-minute, 1954, Douglas County, southwestern Oregon. White Tail Ridge formation (unknown member). Age: Middle early Eocene ("Capay Stage" but near the "Capay Stage"-"Domengine Stage" boundary). Collectors: D. W. Scharf & W. P. Popenoe, 3 September 1930; R. L. Squires, 10–11 July 1988. [= UCMP locs. A-661 & A-662].

LACMIP 24258. Approximately at sharp bend in a short, paved road that leads from Highway 33 to Matilija Hot Springs, NE ¼ of the SE ¼ of section 29, T. 5 N, R. 23 W, U.S. Geological Survey Matilija Quadrangle, 7.5-minute, 1952 (photorevised 1967), Ventura County, southern California. Matilija Sandstone. Age: Early middle Eocene ("Transition Stage"). Collectors: E. C. Jestes, 1963; R. L. Squires, 1990 and 1996.

SDSNH 3278. At 4760 Murphy Canyon Road, at elevation of 104 m (340 ft.) on W side of Murphy Canyon, 5746 m (18,850 ft.) S and 610 m (2000 ft.) E of NW corner of La Mesa Quadrangle, U.S. Geological Survey La Mesa Quadrangale, 7.5-minute, 1967, San Diego County, southern California. Upper part of Scripps Formation. Age: Early middle Eocene ("Transition Stage"). Collector: B. O. Riney, 23, February 1985. [A retaining wall now covers the collecting site].

UCMP 3311. Information from Kew (1924:29): On point of ridge at edge of Simi Valley, south side of Simi Valley, 1.6 km (1 mi.) N and O .13 km (0.08 mi.) W of SE corner of Piru quadrangle, Ventura County, southern California. Collector: B. L. Clark. Information from UCMP locality registry: Simi Hills, Simi Valley, Ventura County, southern California.

UCMP 3586. At elevation of 99 m (325 ft.), on ridge immediately SE of Kellogg Creek, 302 m (990 ft.) N of NE corner of section 12, T. 1 S, R. 2 E, U.S. Geological Survey Byron Hot Springs Quadrangle, 7.5-minute, 1953 (photorevised 1968), Contra Costa County, northern California. Margaret Hamilton Sand [= division D of Meganos Formation as used by Clark & Woodford (1927)]. Age: Early Eocene ("Meganos Stage"). Collector: A. O. Woodford, circa 1920s.

UCMP A-661. See LACMIP loc. 7206.

UCMP A-662. Five meters stratigraphically higher than UCMP loc. A-661.

UCMP A-1154. At elevation of 671 m (2200 ft.), on NE face of ridge marked by prominent red-sandstone capping on W side of Griswold Canyon, near center of W edge of section 23, T. 16 S, R. 10 E, U.S. Geological Survey Panoche Quadrangle, 7.5-minute, 1969, San Benito County, central California. Domengine Formation. Age: Late early to early middle Eocene ("Domengine Stage"). Collector: H. E. Vokes, 1930s.

UCMP A-1547. Dark sandstone interbedded with basalt

at base of sea cliff on small point about 183 m (600 ft.) due N of hill 108 on W side of Crescent Bay, approximately center of section 20, T. 31 N, R. 8 W, U.S. Geological Survey Joyce Quadrangle, 7.5-minute, 1950 (photorevised 1979), Clallam County, Olympic Peninsula, southwestern Washington. Crescent Formation. Age: Middle early Eocene ("Capay Stage"). Collectors: S. A. Berthiaume & Mr. Bramkamp, 1935. [= UCMP loc. A-1548 (approximately) and UCMP loc. A-3212].

UCMP A-1550. About 30 m (100 ft.) S of small cove on W side of Crescent Bay and about 183 m (600 ft.) due E of hill 108 on W side of Crescent Bay, east central part of section 20, T. 31 N, R. 8 W, U.S. Geological Survey Joyce Quadrangle, 7.5-minute, 1950 (photorevised 1979), Clallam County, Olympic Peninsula, southwestern Washington. Crescent Formation. Age: Middle early Eocene ("Capay Stage"). Collectors: S. A. Berthiaume & Mr. Bramkamp, 1935.

UCR 4696. On U.S. Forest Service hiking trail from Fishbowls Campground to Pine Mountain Lodge, 396 m (1300 ft.) S and 122 m (400 ft.) W of NE corner of section 12, T. 6 N, R. 22 W, U.S. Geological Survey San Guillermo Quadrangle, 7.5-minute, 1943, Ventura County, southern California (Givens, 1974:97). Uppermost tongue of siltstone facies of Juncal Formation. Age: Early middle Eocene ("Transition Stage"). Collector: C. R. Givens, circa late 1960s.

UCR 4930. Light gray siltstone containing scattered pebbles and small cobbles, near base of sea cliff 120 m (394 ft.) S of end of beach access road in Blacks Canyon, 3.74 km (2.32 mi.) N, 7.66 km (4.75 mi.) E in zone 11 of UTM grid system, U.S. Geological Survey Del Mar Quadrangle, 7.5-minute, 1967, San Diego County, southern California. Ardath Shale. Age: Late early to early middle Eocene ("Domengine Stage"). Collector(s): Unknown.

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THE VELIGER

A New Subgenus and a New Species of *Holospira* (Gastropoda: Pulmonata: Urocoptidae) from Sonora, Mexico

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Abstract. *Holospira* (***Millerella***) ***hoffmani*** Gilbertson & Naranjo-García, sp. nov. from the Sierra Batamote of eastern Sonora, Mexico, and the new subgenus ***Millerella*** are described. *Holospira milleri* Gilbertson, 1989, is transferred from *Holospira, sensu stricto* to ***Millerella*** subgen. nov.

INTRODUCTION

Several holospiras have been described from the northwestern Mexican state of Sonora. Species representing four (of seven) subgenera are extant in this state alone (Gilbertson, 1993), including *Holospira, sensu stricto* von Martens, 1860; *Allocoryphe* Pilsbry, 1953; *Eudistemma* (Dall, 1896); and *Sonoraloa* Gilbertson, 1993. With the exception of *Sonoraloa,* these subgenera were described solely on the basis of shell characters.

Recent investigations have focused on variations of the reproductive organs of holospiras from this region. Data gleaned from these studies have been useful in classification, especially at the subgeneric level (Gilbertson, 1993). In this regard, the present new species exhibits a reproductive anatomy that is unlike that of all of the other *Holospira* species for which the anatomy is known except that of *H. milleri* Gilbertson, 1989, another Sonoran species.

MATERIALS AND METHODS

Three snails were drowned and their shells were broken carefully and removed, leaving the soft anatomy intact. The reproductive system of each snail was then dissected free from the other internal organs. It was stained with Delafield Hematoxylin, destained with 3% acid alcohol, counter-stained with Eosin-Y, and placed between a slide and a cover slip. Then it was dehydrated in a series of three changes (jars) of absolute ethanol and, for clearing, in a change of 50% absolute ethanol and 50% toluene and three more changes of 100% toluene. The stained reproductive system was then permanently slide-mounted in Permount (Gregg, 1959; Naranjo-García, 1989).

SYSTEMATICS

Family UROCOPTIDAE Pilsbry & Vanatta, 1898

Subfamily HOLOSPIRINAE Pilsbry, 1946

Genus *Holospira* von Martens, 1860

Subgenus ***Millerella*** Gilbertson & Naranjo-García, subgen. nov.

Type species: *Holospira milleri* designated herein. It is transferred from *Holospira, sensu stricto.*

Distribution: Mexico, east-central Sonora.

Diagnosis: Shell umbilicate, cylindroconic to turriform in shape. Embryonic whorls rounded, tapering toward apex. Internal column moderately slender to slender, lamellate. Armature of three to four lamellae in penultimate whorl. Male genitalia with short, conic verge present in small penial sac; epiphallus limited to short enlargement of vas deferens atop penial sac. Vagina and spermathecal diverticulum lacking.

Etymology: This subgenus is named for Dr. Walter B. Miller, a distinguished student of North American land snails and a generous mentor.

Remarks: The new subgenus is erected for the trilamellate *H.* ***hoffmani*** sp. nov. and the quadrilamellate *H. milleri* in order to reflect the similarities in many of their shell features and their nearly identical reproductive anatomies. The removal of *H. milleri* from *Holospira, sensu stricto* represents a partial revision of the nominate subgenus.

Holospira, sensu stricto is defined solely by the presence of all four internal lamellae (axial, parietal, basal, and palatal) in the penultimate whorl of the shell (see Pilsbry, 1903:72; 1946:115). However, this singular cri-

terion is superficial and results in a "form-subgenus." Recognizing this, Pilsbry later (1953:141) stated: "There is considerable diversity in size, shape and sculpture (of *Holospira, sensu stricto*), and probably several subgenera will eventually be recognized." (The nominate subgenus is still represented in Sonora by *H. cyclostoma* Pilsbry, 1953. However, this species is known only from shell material extracted from river drift. Analysis of its internal organs is not possible until living populations are located.)

The other subgenera of *Holospira* are characterized by species that exhibit only one internal lamella (the axial), or none, except for *Eudistemma* (see Bequaert & Miller 1973:138) and *Prionoplax* Pilsbry, 1953. In *Eudistemma,* species may have one, two, or three lamellae (axial, basal, parietal) in the penultimate whorl and they often show great intraspecific variability with respect to their number, strength, and length. Some specimens of *H. (E.) crossei* Dall, 1895, and *H. (E.) montivaga* Pilsbry, 1946, are even alamellate (Pilsbry, 1946:122). *Prionoplax* is trilamellate, but the parietal lamella is three to four whorls long and serrate. The only species, *H. (P.) odontoplax* Pilsbry, 1953, would have been placed in genus *Propilsbrya* Bartsch, 1906, which it otherwise resembles, except for the presence of a basal lamella.

The embryonic whorls of ***Millerella*** are rounded, unlike those of *Allocoryphe* in which they are characteristically angular at the upper-outer margin giving a flattened, straight-sided appearance. Also, these whorls increase in width (taper toward apex) unlike those of *H. kinonis* Baily & Baily, 1940, a species collected in river drift near Guaymas, Sonora (subgeneric status uncertain; Gilbertson, 1993) in which they are of nearly equal size.

The reproductive systems of 16 *Holospira* spp. representing five of the seven subgenera (*Allocoryphe*; *Bostrichocentrum* Strebel & Pfeiffer, 1880; *Eudistemma*; *Holospira, sensu stricto*; and *Sonoraloa*) have been published (Gilbertson, 1989a,b, 1993; Pilsbry 1903:70–71, pls. 19, 27; Thompson, 1964). This system is also known from *H. mesolia* Pilsbry, 1912 (personal observation, LHG), which is assigned to *Haplocion* Pilsbry, 1902. The male anatomy of ***Millerella*** differs from the anatomies of these other subgenera in two distinct respects: (1) it exhibits a verge in the penial sac and (2) it lacks a tubular epiphallus. The lack of a tubular epiphallus results in a very short distal portion of the male duct system. In addition, ***Millerella*** lacks the spermathecal diverticulum (appendix) of the female system characteristic of *Bostrichocentrum, Eudistemma,* and two (of three) species of *Holospira, sensu stricto* for which the anatomy is known (*H. nelsoni* Pilsbry, 1903 and *H. sherbrookei* Gilbertson, 1989). The one remaining species of the nominate subgenus that has been anatomically described, *H. goldfussi* (Menke, 1847), lacks this diverticulum but exhibits a "capacious vagina" (Pilsbry, 1903).

Holospira (***Millerella***) ***hoffmani*** Gilbertson & Naranjo-García, sp. nov.

(Figures 1–3)

Diagnosis: Shell small for genus, umbilicate, cylindroconic to turriform in shape, trilamellate. Internal column moderately slender, lamellate. Embryonic whorls rounded; whorls of cone convex. Male genitalia with short, non-tubular epiphallus and a conic verge in small penial sac.

Description of shell of holotype (Figure 1A, B, D): Shell moderately small for genus, umbilicate, cylindroconic in shape with slightly convex spire merging very gradually into cone, cream in color. Whorls 11.5 in number. Embryonic whorls 2.3 in number, rounded, minutely granular, tapering toward apex. Whorls of the cone approx. 5 in number, convex with greatest diameter below midline giving a somewhat sloping appearance. Whorls of cylindric portion also convex with greatest diameter near midline. Retractively slanted ribs prominent on all post-embryonic whorls, with intercostal spaces approx. 1.5 width of rib. Ribs smoother on cylindric whorls. Aperture slightly auriculate; peristome expanded (except at upper-outer margin) and slightly extended from body whorl. Greatest length 9.6 mm; greatest width 3.5 mm. Umbilicus 0.6 mm in diameter.

Internal shell structure (Figure 1C): Internal column moderately slender (approx. 0.17 diameter of shell in third whorl), hollow, not enlarging apically, with strong lamella in penultimate whorl above aperture (approx. 0.5 of whorl). Parietal lamella well developed, flaring outward (approx. 0.3 of whorl); basal lamella weak (approx. 0.3 of whorl). Palatal lamella lacking.

Variations of paratypes: Thirty-six paratypes range from short and conic (8.2 × 3.5 mm) to elongate and turriform (11.2 × 3.4 mm). They average 9.7 mm in greatest length and 3.5 mm in greatest diameter.

Sixty additional shells (SBMNH No. 74815) from a nearby location (within approx. 1 km) exhibit a more pronounced slope of the body whorls giving the appearance of overhanging at the sutures. These shells were collected by W. B. and W. N. Miller on 19 August 1965. (Locality data on label as follows: Sonora, N of Mina El Milagro, Sierra del Santo Nino, 12.7 mi. [21.2 km] from lower bridge at El Novillo [toward] Sahuaripa; in limestone rocks; ca. 4,000 ft.)

Description of reproductive anatomy: Description based on specimen illustrated in Figures 2, 3 (Santa Barbara Museum of Natural History slide no. 143994). Vas deferens enlarging into epiphallus only as it enters penial complex. Penial sac (penis) very short, narrowing basally, with small, apical, conic verge (slanting in illustrated specimen). Penial retractor muscle moderate in size, inserting atop penial sac adjacent to entrance of epiphallus.

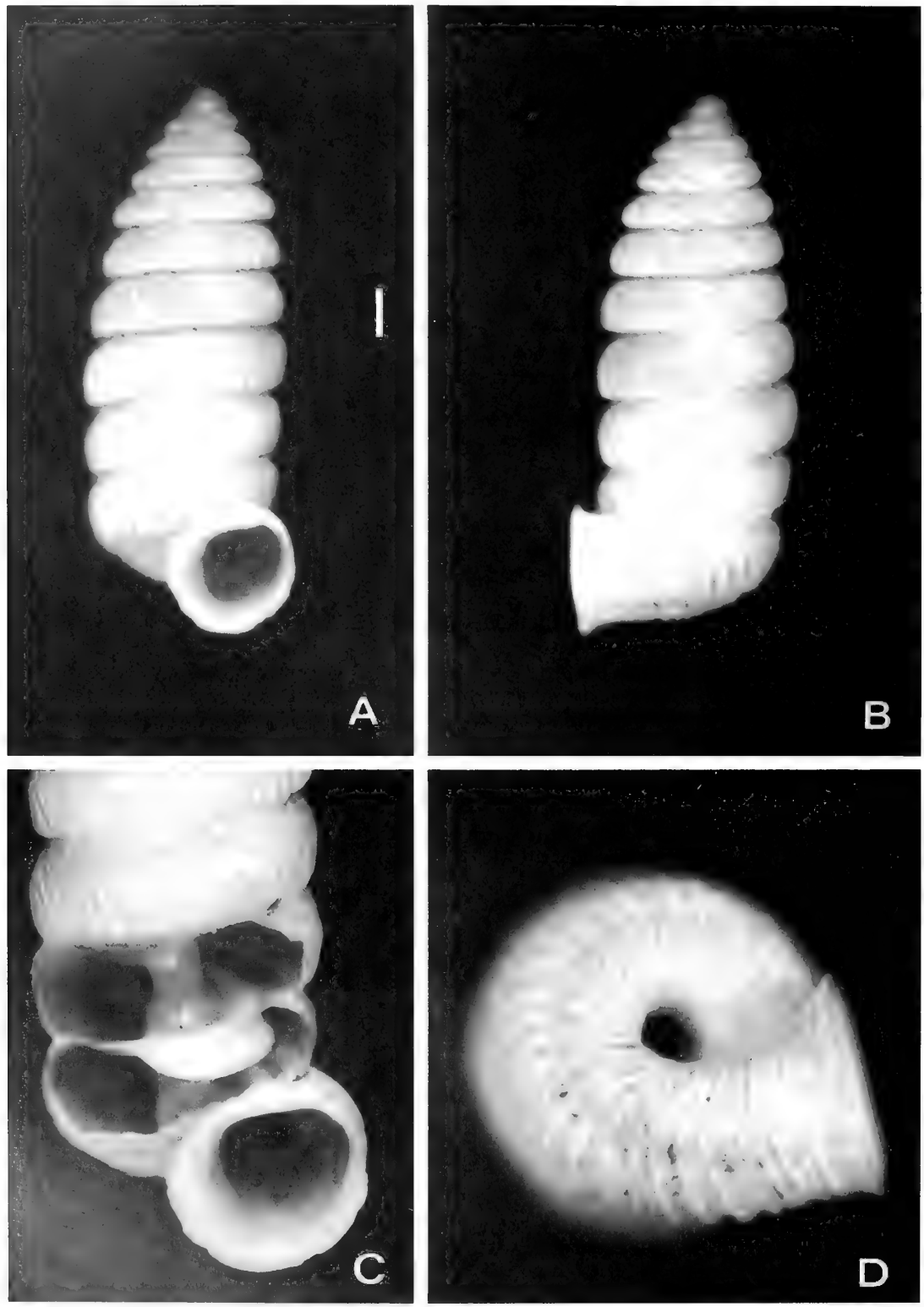

Figure 1

Holospira ***hoffmani*** Gilbertson & Naranjo-García, sp. nov., holotype, Santa Barbara Museum of Natural History No. 143186, apertural view (A), side view (B), and basal view (D). C. Internal view of paratype. Scale bar for A and B = 1 mm.

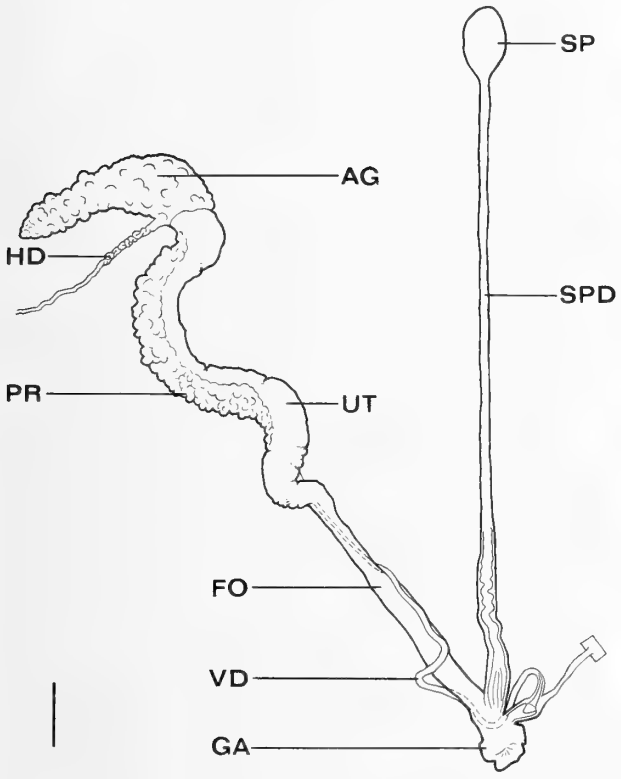

Figure 2

Reproductive system of *Holospira* ***hoffmani*** Gilbertson & Naranjo-García, sp. nov. Specimen collected at type locality, 3 January 1988. SBMNH slide No. 143994. Abbreviations: AG, albumen gland; FO, free oviduct; GA, genital atrium; HD, hermaphroditic duct; PR, prostate gland; SP, spermatheca; SPD, spermathecal duct; UT, uterus; VD, vas deferens. Scale bar = 1 mm.

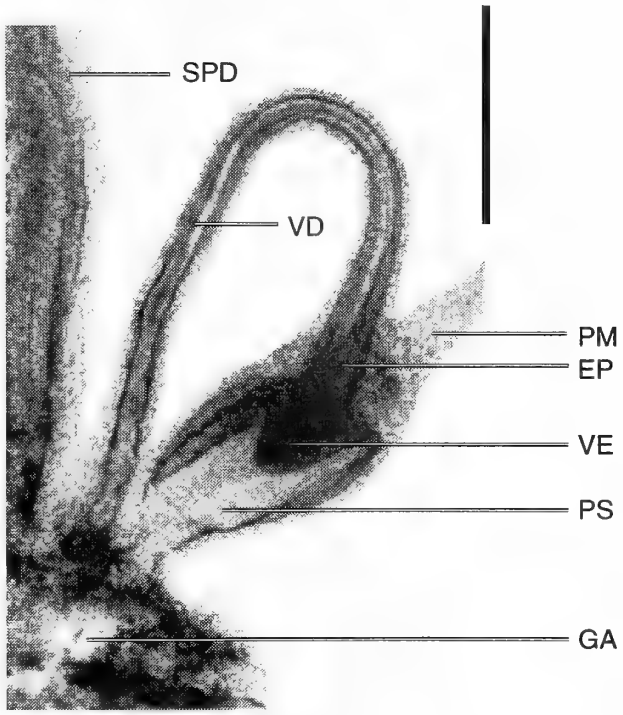

Figure 3

Male genitalia of *Holospira* ***hoffmani*** Gilbertson & Naranjo-García, sp. nov. SBMNH slide No. 143994. Abbreviations: EP, epiphallus; GA, genital atrium; PS, penial sac (penis); PM, penial retractor muscle; VD, vas deferens; VE, verge. SPD, spermathecal duct of female system. Scale bar = 0.4 mm.

Spermathecal duct enlarging basally with internal, undulated section immediately above base. Spermatheca ovoid; spermathecal diverticulum lacking. Free oviduct expanded with undulating vas deferens alongside. Uterus typical with attached prostate gland. Hermaphroditic duct entering albumen gland near base.

Type locality: Mexico, east-central Sonora, Sierra Batamote (near El Milagro Mine), 20.5 km E of the Rio Yaqui Bridge along Hwy. 15 from La Estrella to Bacanora, 28°57.5′N, 109°30.5′W, approx. 1070 m elevation.

This is a fairly steep, rocky, south-facing slope beneath cliffs. Snails were found estivating under surface rocks (3 January, 1988). Specimens of *Holospira remondi laevior* Pilsbry, 1953, were collected at the same site (see Gilbertson, 1993:73).

Etymology: This species is named for our friend and colleague, southwestern (U.S.) malacologist, Dr. James E. Hoffman.

Disposition of types: Holotype: Santa Barbara Museum of Natural History No. 143186. Paratypes: Academy of Natural Sciences of Philadelphia No. 399396, Florida Museum of Natural History No. 264417, Los Angeles County Museum of Natural History No. 2805, National Museum of Natural History—Smithsonian Institution No. 860750, Santa Barbara Museum of Natural History No. 74815, Universidad Nacional Autónoma de México, Colección Nacional Mollusca No. 533, University of Texas at El Paso No. 13628, Edna Naranjo-García Collection No. 642.

Remarks: *Holospira* (***Millerella***) ***hoffmani*** resembles *H. milleri* with regard to the morphology of several shell features including that of the embryonic whorls, internal lamellae (except palatal), peristome, aperture, and umbilicus. Conversely, these two species differ from each other in four main respects: (1) the shape of their post-embryonic whorls (*H. milleri* exhibits extremely convex, subcarinate, post-embryonic apical whorls), (2) rib thickness (*H. milleri* is more finely rib-striate), (3) number of internal lamellae, and (4) shell size and shape (*H. milleri* is longer and more turriform). Also, the internal column and umbilicus are somewhat more narrowed in *H. milleri.*

The reproductive systems of *Holospira* ***hoffmani*** and

H. milleri are nearly identical. However, *H. milleri* exhibits a slightly longer and more narrowed spermathecal duct and a reniform (rather than ovoid) spermatheca.

ACKNOWLEDGMENTS

We thank James E. Hoffman and Walter B. Miller for accompanying us to Sonora when specimens of the present new species were collected. Dr. Miller discovered the nearby population several years earlier while doing studies on the genus *Sonorella.* We also thank Dwayne L. Moses for assistance with the preparation of the figures herein and Paul H. Scott of the Santa Barbara Museum of Natural History for the loan of shell material.

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Ichnusomunda sacchii, a New Hygromiid Snail from Sardinia Island (Western Mediterranean): An Intriguing Case of Homoplasy in the Anatomical Organization (Pulmonata: Hygromiidae)

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Abstract. ***Ichnusomunda sacchii,*** new genus and new species, is described from Sardinia. The new genus is anatomically characterized by: right ommatophore retractor independent of genitalia; penial nerve from right pedal ganglion; left lateral lobe of pallial margin long; vagina with digitiform glands and 0 + 2 dart-sac complex, the latter consisting of elongated, wide, cylindrical basal portion, joined perpendicular to distal vagina, at the apex of which two stylophores open side-by-side; outer stylophore small, globular, with thick, muscular walls, secreting dart; inner stylophore long and slender, with thin walls and wide, empty (dartless) lumen, bent to adhere to upper side of basal portion; penis with long, cylindrical penial papilla having three basal frenula. This combination of anatomical characters is unique and distinct from those in the other genera of the Hygromiidae. Some of these characters (pedal penial innervation; three frenula at the base of penial papilla) are shared with *Cernuella* (*Cernuella*) and *Cernuella* (*Xeroamanda*), others (basal portion of dart-sac complex; structure of inner stylophore) with *Xeromunda, Xerolenta,* and *Pseudoxerophila.*

I. sacchii has a limited distribution, being known only from the type locality, the sand dunes of Riu Piscinas, a very important biotope of western Sardinia (no. 20/35 in the checklist of the Società Botanica Italiana; no. ITB000031 of the "Nature-2000 Web"). Although ***I. sacchii*** is very common in this site, its limited distribution is a clear risk factor in the face of man-made modifications to the peculiar habitat in which it lives.

INTRODUCTION

Sardinia and Corsica have a rich hygromiid fauna characterized by a number of endemic taxa, e.g., *Cyrnotheba corsica* (Shuttleworth, 1844), *Ichnusotricha bernini* Giusti & Manganelli, 1987, *Nienhuisiella antonellae* Giusti & Manganelli, 1987, *Xerosecta dohrni* (Paulucci, 1882), *X. hillyeriana* (Paulucci, 1882), and others with a reduced disjunct distribution, e.g., the Tyrrhenian *Tyrrheniellina josephi* (Giusti & Manganelli, 1990), and the West Mediterranean *Ganula lanuginosa* (Boissy, 1835) and *Polloneriella contermina* (Pfeiffer, 1847) (Carrada et al. 1967; Giusti & Castagnolo, 1983; Giusti & Manganelli, 1987, 1989; Manganelli et al., 1995).

The recent study of material collected in dune habitats by Prof. C. Sacchi of the Dipartimento di Biologia of the University of Pavia (Italy) has led to the identification of another, previously unknown xerophilous hygromiid, very peculiar in the structure of the distal genitalia.

MATERIALS AND METHODS

Whole shells were photographed under the light microscope (Wild M5A). All dimensions (shell height, maximum shell diameter, aperture height, and aperture diameter) were measured using calipers.

Living specimens were drowned in water, then fixed and preserved in 75% ethanol, buffered with $NaHCO_3$. The bodies were isolated after crushing the shells, and dissected under the light microscope (Wild M5A) using very thin pointed watchmaker's tweezers. Anatomical details were drawn using a Wild camera lucida. Anatomical parts were measured using a millimetric lens on the same microscope.

Radulae were manually extracted from the buccal bulbs, washed in pure 75% ethanol, mounted on copper blocks with conductive glue, sputter-coated with gold, and studied using a Philips 505 SEM.

The material examined is listed as follows: locality, municipality, and province names in parenthesis, UTM reference, collector(s), date, number of specimens in parenthesis. Locality names were according to the official 1:25,000 scale map of Italy (series M 891, sheet 225 IV SO) and UTM references were according to the official 1:100,000 scale map of Italy (series M 691, sheet 224–225).

Unless otherwise indicated, all the specimens illustrated are kept in the Giusti Collection (Dipartimento di Biologia Evolutiva, Via Mattioli 4, I-53100 Siena, Italy).

SYSTEMATICS

Ichnusomunda Giusti & Manganelli, gen. nov.

Type species: ***Ichnusomunda sacchii*** sp. nov.

Diagnosis: Pulmonate, hygromiid snail with shell dextral, small, globose, and anatomically characterized by: (1) right ommatophore retractor independent of genitalia; (2)

penial nerve from right pedal ganglion; (3) left lateral lobe of pallial margin long; (4) vagina with digitiform glands and 0 + 2 dart-sac complex, the latter consisting of elongated, wide, cylindrical basal portion, perpendicularly joined to distal vagina, at whose apex two stylophores open side-by-side; outer stylophore small, globular, with thick, muscular walls, secreting dart; inner stylophore long and slender, with thin walls and wide, empty (dartless) lumen, bent to adhere to upper side of basal portion; (5) penial complex consisting of flagellum, epiphallus and penis; penis with long, cylindrical penial papilla having three basal frenula.

Origin of the name: *Ichnusomunda,* gender feminine, is derived from "Ichnusa," the Latin name of Sardinia (in Pliny), and the suffix "munda" from *Xeromunda,* the Mediterranean, hygromiid genus superficially (conchologically), most similar to the new genus.

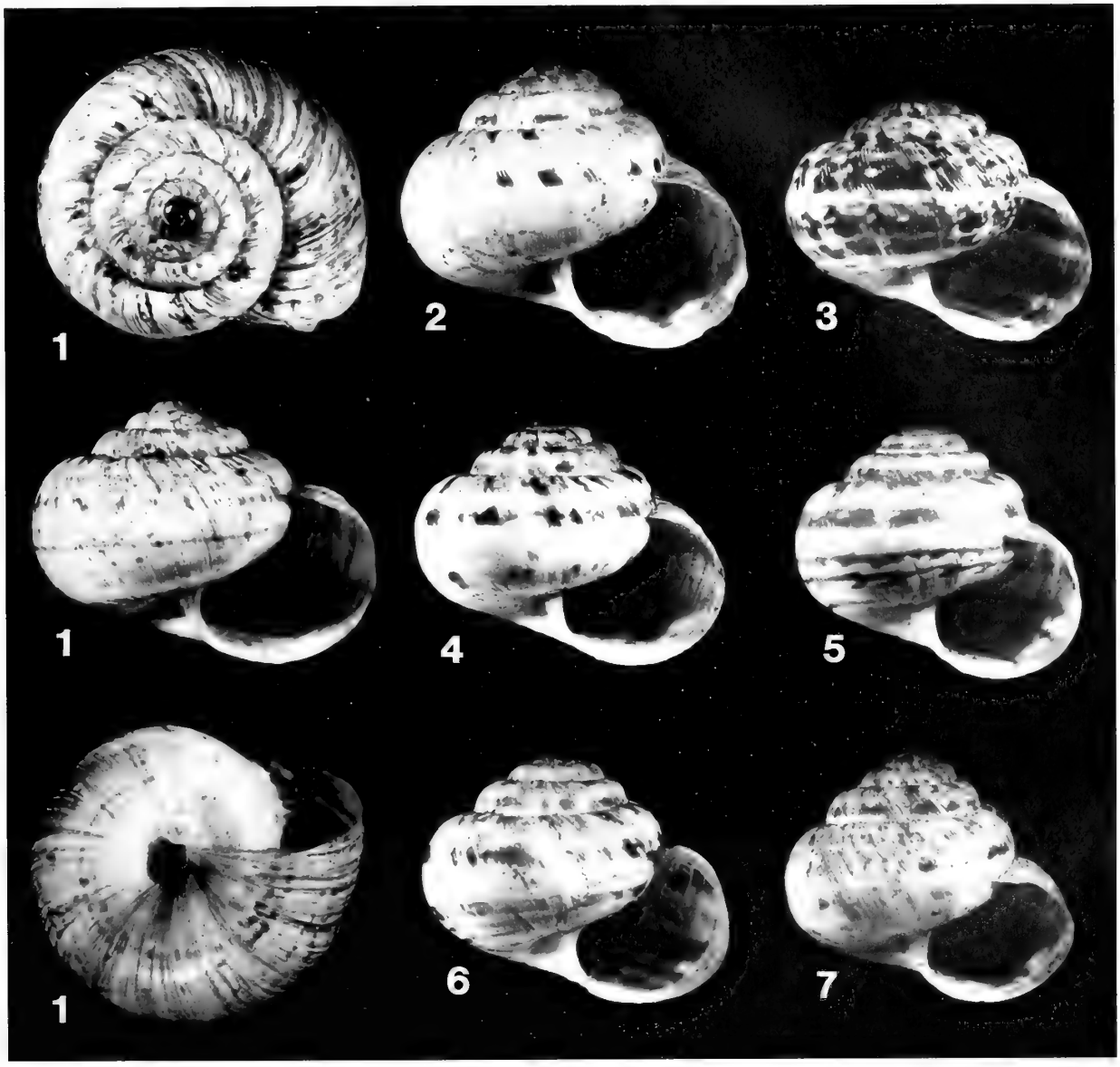
Ichnusomunda sacchii Guisti & Manganelli, sp. nov.

Diagnosis: ***Ichnusomunda sacchii*** is the only known species of the genus ***Ichnusomunda.*** Consequently its diagnosis is the same as that of the genus.

Shell (Figures 1–7): dextral, globose, small, hairless, whitish, with two to eight ginger brown bands usually fragmented into rows of spots of variable size, with very fine, regularly spaced riblets clearly visible from sutures to periphery of whorls, and fading out from periphery of last whorl to umbilicus (this portion consequently has a smooth appearance). Spire conical, consisting of 5 ⅛–5 ⅓ (in fully adult specimens; protoconch consisting of ca. 1 ¾ whorls) convex, regularly increasing whorls separated by deep sutures; last whorl slightly dilated and sometimes descending slightly near aperture. Umbilicus open, very small, partly covered by reflected columellar margin of peristome. Aperture oblique, usually rounded, rarely slightly elliptical or squared, with very thin to absent internal rib. Peristome not thickened, slightly reflected at lower and columellar margin (with upper vertex starting at, or just above, periphery of last whorl). Dimensions (N = 50). Shell diameter: 8.8 ± 0.8 mm (range: 7.8–10.3 mm); shell height: 7.3 ± 0.7 mm (range: 6.5–8.8 mm); aperture diameter: 5.2 ± 0.5 mm (range: 4.6–6.0 mm); aperture height: 4.3 ± 0.4 mm (range: 3.9–5.3 mm).

Body (Figures 8–9): Soft parts yellowish to pale pinkish. Mantle border with five lobes: right and left dorsal bordering upper margin of pneumostome, not particularly long; left lateral long, in form of thin lamina with upper vertex ending quite close to apex of left dorsal; subpneumostomal, variable in shape, usually triangular; right lateral, elongated triangular with base situated just below anal opening. Mantle border rather angled at right upper vertex; foot with non-partite sole of holopode type; walls of pallial cavity colorless, or with small black stripes or spots (larger spot close to mantle border near pneumostome and anus; transverse stripes border minor, transverse vessels; one longitudinal line along pulmonary vein).

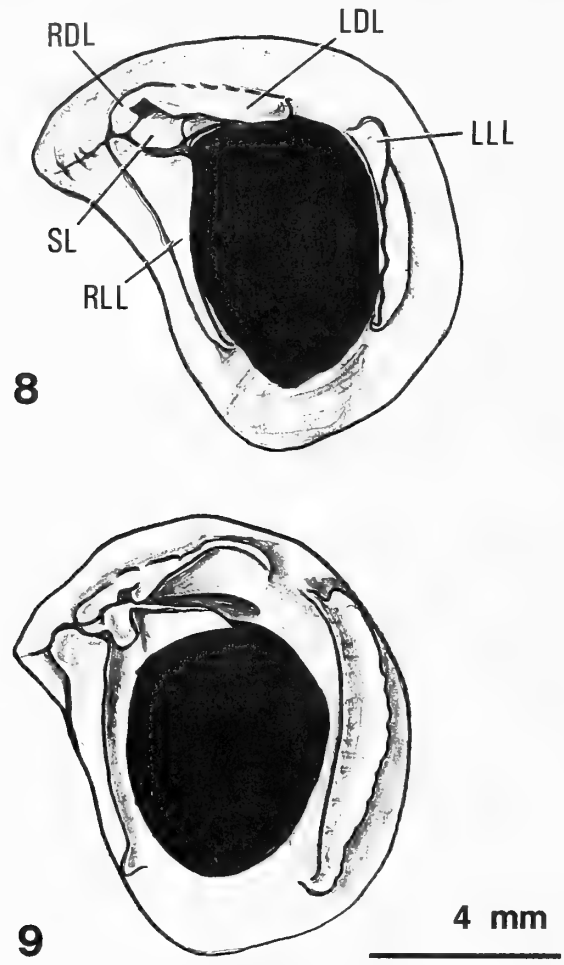
Genitalia (Figures 10–22): Eight specimens dissected (five of which measured): General scheme of the semidiaulic monotrematic type. Large hermaphrodite gonad (ovotestis) consisting of acini, ducts of which converge into first hermaphrodite duct having initial portion very slender, then widening to function as seminal vesicle. First hermaphrodite duct ending in clublike "talon" adhering to internal side of large, beanlike albumen gland. Talon consisting of two distinct structures, one long, slender (digitlike), outward-projected, containing seminal receptacles (treelike system of tubules, ending in three to four branches), other, functioning as fertilization chamber, globose (saclike), with thin walls and wide lumen. Second hermaphrodite duct (ovispermiduct) arising from base of albumen gland, and consisting of female channel (uterine portion of ovispermiduct containing seminal groove) and prostate gland (with sperm groove) fused to define single lumen. Short (1.6–2.6 mm) free oviduct following female channel. Duct of bursa copulatrix arising from where proximal vagina follows free oviduct, long (6.8–8.1 mm), initially not or very slightly flared, ending in large, ovoidal to saclike bursa copulatrix (gametolytic gland). Long slender, externally smooth, apically pointed, oval in transverse section spermatophore sometimes present inside duct of bursa copulatrix and bursa copulatrix. Proximal vagina in two parts: one (from where duct of bursa copulatrix begins to base of digitiform glands) very short (0.6–0.7 mm), other (from base of digitiform glands to where basal portion of dart-sac complex enters vagina) longer (1.6–3.0 mm). Three to four tufts of branched, long, slender digitiform glands arising from vagina, one to two tufts opposite other two. Elongated dart-sac complex (DSC) entering distal vagina at right angle, and having two stylophores, on same side of vagina (0 + 2 DSC); dart-sac complex consisting of wide, cylindrical basal portion (2.6–3.2 mm) at apex of which two stylophores opening side-by-side; on internal upper wall of basal portion two large pleats originating in proximal vagina distally fusing to form calotte covering outer stylophore opening (and dart tip when dart present); kind of pleat of pale yellowish glandular tissue bordering distal portion of pleats and calotte, also visible from outside; outer stylophore small (length about 0.6–0.7 mm), globular, with thick, muscular walls and small, short lumen in which dart secreted; dart very short (0.6–0.7 mm), oval in transverse section near base, spear-shaped (with one lateral wing on opposite sides) and lenslike in transverse section at tip; inner stylophore ("nebensack" or accessory sac), difficult to discern externally because bent toward vagina and fastened to upper side of basal portion by strips of tissue; when strips removed, inner stylophore revealing long (2.0–2.4 mm), clublike, sometimes slightly twisted



Explanation of Figures 1 to 7

Shells of ***Ichnusomunda sacchii*** Giusti & Manganelli, gen. & sp. nov., from Is Arenas, Cuccuru Pranu (Arbus, Cagliari, Sardinia, Italy), 32SMJ5378, G. Manganelli, L. Manganelli & G. Cappelli leg. 19 October 1995. Holotype (1) in the Museo di Zoologia dell'Università di Firenze (Florenze, Italy), MZUF 11566. Other specimens in Giusti Collection (Dipartimento di Biologia Evolutiva, Via Mattioli 4, I-53100 Siena, Italy). All ×3.5.

with thin walls and rather wide empty cavity. Penial complex consisting of flagellum, epiphallus, and penis; flagellum very short (0.7–0.9 mm), ending level with where vas deferens enters penial complex and epiphallus begins; epiphallus long (6.0–8.2 mm), ending where penial retractor muscle contacts penial complex wall and penis begins; penis (from where penial retractor muscle inserts to distal vagina close to base of genital atrium) about half epiphallus length (3.0–3.7 mm), entering distal vagina, slightly closer to genital atrium than base of dart-sac complex; penis consisting of very short proximal portion (from where penial retractor muscle ends to base of penial papilla; length: 0.6–0.9 mm) and longer distal portion (in which penial papilla lodged; length: 2.4–2.8 mm); penial papilla rather long (2.0–2.5 mm), conical, with three basal frenula connecting it to inner surface of penis wall, having apical opening, transverse section of which revealing compact structure (only one, small lacuna half-



Explanation of Figures 8 and 9

Mantle border of two specimens of ***Ichnusomunda sacchii*** Giusti & Manganelli, gen. & sp. nov., from Is Arenas, Cuccuru Pranu (Arbus, Cagliari, Sardinia, Italy), 32SMJ5378, G. Manganelli, L. Manganelli & G. Cappelli leg. 19 October 1995. Giusti Collection (Dipartimento di Biologia Evolutiva, Via Mattioli 4, I-53100 Siena, Italy). Key: LDL, left dorsal lobe; LLL, left lateral lobe; RDL, right dorsal lobe; RLL, right lateral lobe; SL, subpneumostomal lobe.

way between outer wall and lumen); fascia containing pale yellowish glandular tissue (difficult to discern from outside), bordering opening of penis into distal vagina, and forming sphincterlike ring; genital atrium very short (1.0–1.6 mm), opening on right side of body near base of right ommatophore; large, raised, crestlike, pleat (possibly "organ of contact" similar to that in other hygromiids and helicids) on internal wall of genital atrium on same side as penis enters genital atrium.

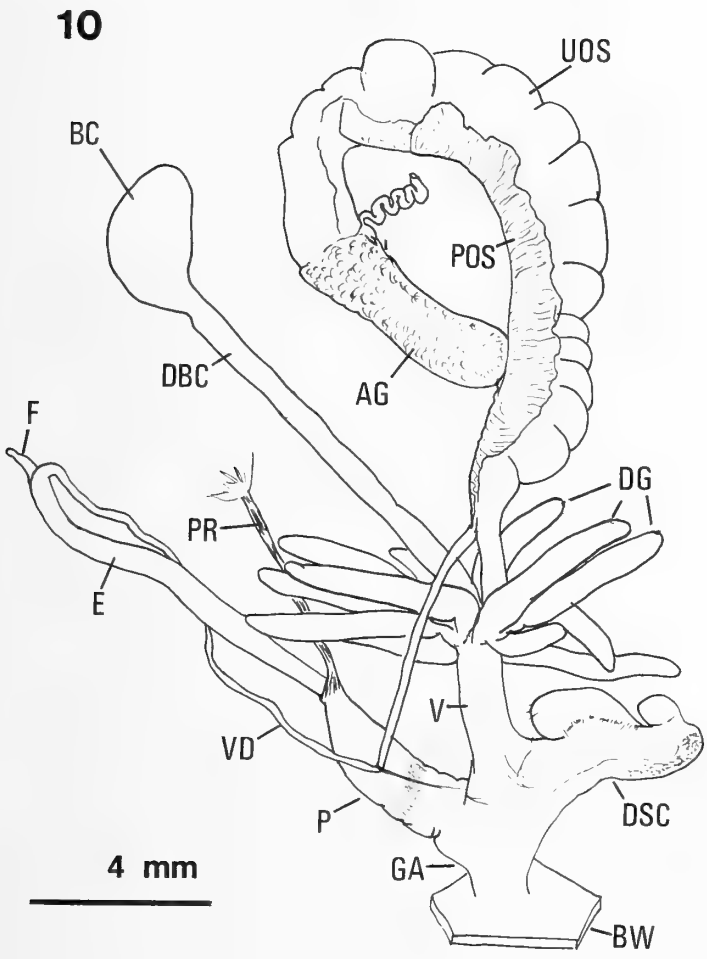
Radula: Consisting of many rows each of about 45–47 teeth; central tooth with large tricuspid crown, mesocone more than twice ectocone height; first lateral teeth with bicuspid crown, mesocone long and robust, inner side of mesocone somewhat milled, ectocone small (ca. one-half mesocone height) and sharply pointed; last lateral teeth with bicuspid crown, mesocone long with very small indentation on inner side at about two-thirds of mesocone height, ectocone small, slender, and sharply pointed; latero-marginal teeth with bicuspid crown, mesocone more slender than in lateral teeth, with small protuberance on inner side at about two-thirds of mesocone height, ectocone small, slender and sharply pointed; extreme marginal teeth with crown composed of mesocone, usually with one to two small protuberances on inner side and still evident ectocone, frequently split into two to three small, sharp points.

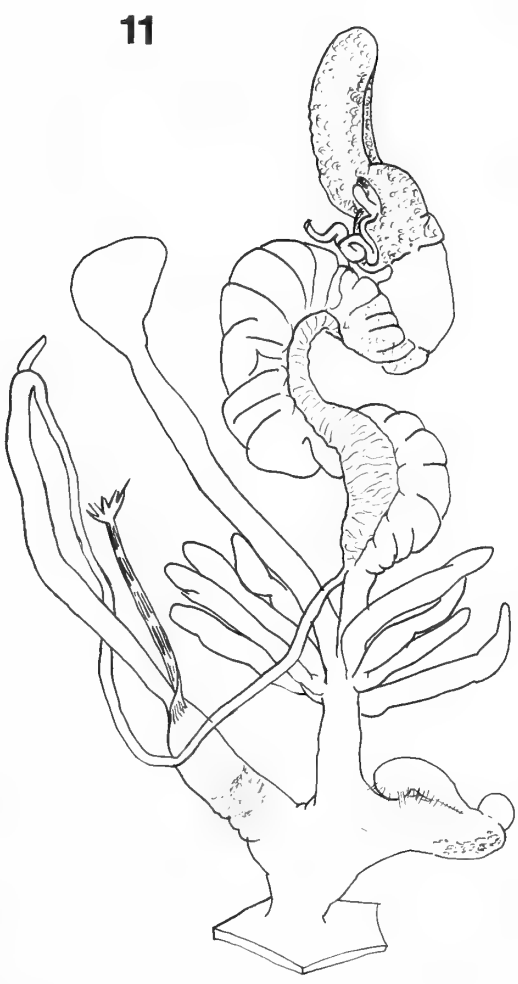
Type locality: Sardinia Island, Is Arenas, Cuccurru Pranu (municipality of Arbus, province of Cagliari), 32TMJ5378.

Type material: Holotype from Is Arenas, Cuccuru Pranu (Arbus, Cagliari), 32SMJ5378, G. Manganelli, L. Manganelli & G. Cappelli leg. 19 October 1995 in the Museo di Zoologia dell'Università di Firenze (Florence, Italy), MZUF 11566 and 388 paratypes from the following localities: Is Arenas, near the mouth of Riu di Naracauli (Arbus, Cagliari), 32TMJ5376, G. Manganelli & F. Giusti leg. 17 May 1994 (130 shells); 5 in the Museo di Zoologia dell'Università di Firenze (Florence, Italy), MZUF 11567; 5 in Museo Regionale di Scienze Naturali (Turin, Italy), MRSN 121.1-5. Is Arenas, Sisca (Arbus, Cagliari), 32SMJ5377, G. Manganelli, L. Manganelli & G. Cappelli leg. 18 October 1995 (46 shells and 9 living specimens; 5 shells in the Museo di Zoologia dell'Università di Firenze, MZUF 11568; 5 shells in Museo Regionale di Scienze Naturali, Torino, MRSN 122.1-5). Is Arenas, Cuccuru Pranu (Arbus, Cagliari), 32SMJ5378, G. Manganelli, L. Manganelli & G. Cappelli leg. 19 October 1995 (41 shells and 50 living specimens; 5 shells in Museo Regionale di Scienze Naturali, Torino, MRSN 120.1-5). Is Arenas, Riu Piscinas (Arbus, Cagliari), 32SMJ57 C. Sacchi leg. 18 March 1982 (90 shells and 22 juvenile living specimens).

Origin of the name: The new species is named after Prof. Cesare Sacchi (Pavia, Italy), in appreciation of his friendship and esteem for his many important contributions to the ecology and biogeography of non-marine mollusks of the western Mediterranean.

Taxonomy: Before introducing a new species we checked that a name was already available for the new species among the new names created by past authors for Sardinian hygromiids. Five xerophilous hygromiids (see Table 1; Figures 23–27) have been described from Sardinia. Two of these, *Helix dohrni* Paulucci, 1882, and *Helix hillyeriana* Paulucci, 1882, are *Xerosecta* species (Manganelli et al., 1995). The others are in need of re-





Explanation of Figures 10 and 11

Genitalia (gonad excluded) of two specimens of ***Ichnusomunda sacchii*** Giusti & Manganelli, gen. & sp. nov., from Is Arenas, Cuccuru Pranu (Arbus, Cagliari, Sardinia, Italy), 32SMJ5378, G. Manganelli, L. Manganelli & G. Cappelli leg. 19 October 1995. Giusti Collection (Dipartimento di Biologia Evolutiva, Via Mattioli 4, I-53100 Siena, Italy). Key: AG, albumen gland; BC, bursa copulatrix; BW, body wall; DBC, duct of bursa copulatrix; DG, digitiform glands; DSC, dart-sac complex; E, epiphallus; F, flagellum; GA, genital atrium; P, penis; POS, prostatic portion of ovispermiduct; PR, penial retractor muscle; UOS, uterine portion of ovispermiduct; V, vagina; VD, vas deferens.

vision, but are not related to the new species because they are based on specimens of *C.* (*Cernuella*).

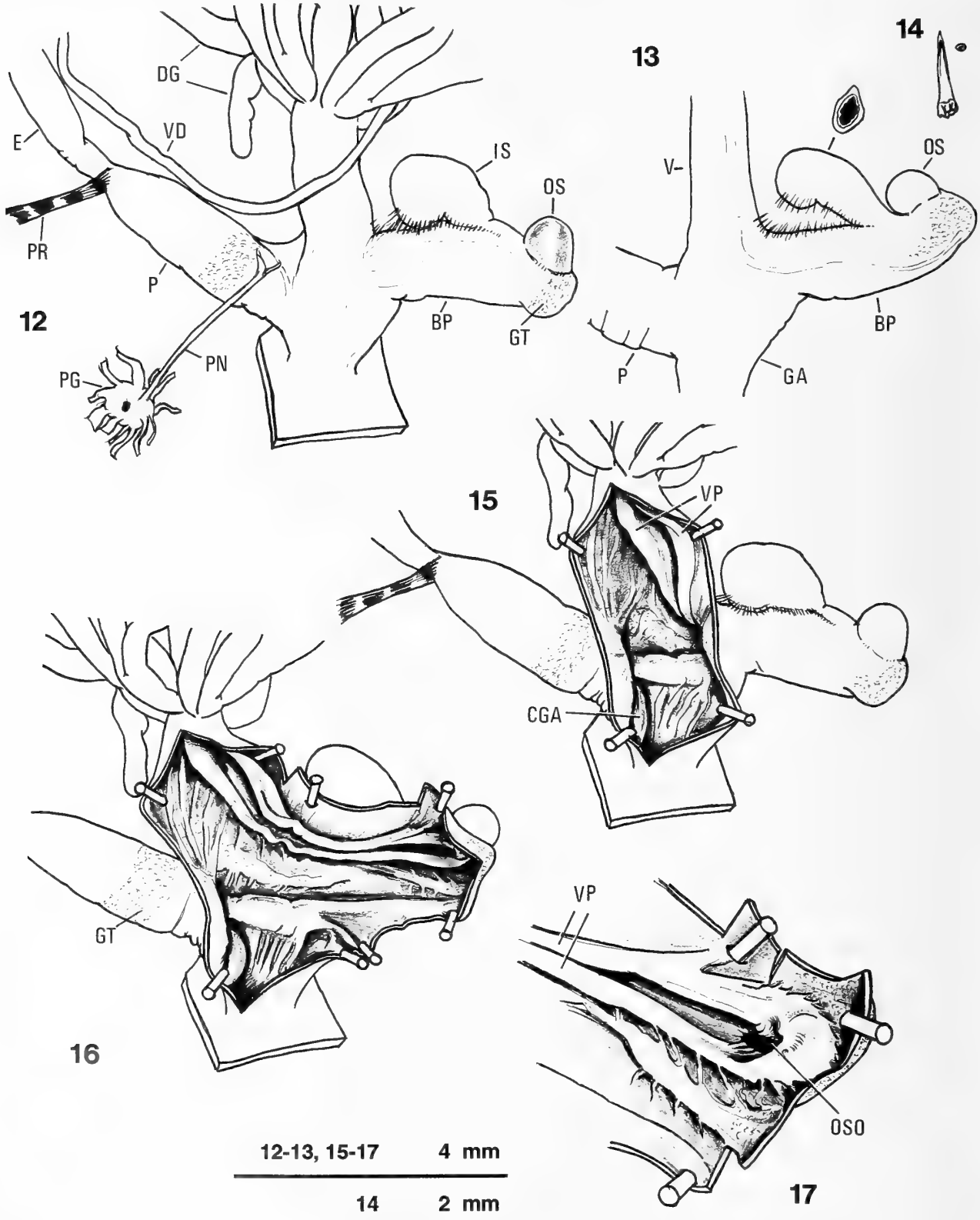
Among these species, that having a shell most similar to ***I. sacchii*** is *H. dohrni,* but anatomical examination of specimens from many localities of northern Sardinia (including the neighborhood of Sassari) proved that this species belongs to the genus *Xerosecta.*

Habitat: Sandy dunes. At base of bushes or under sparse vegetation or litter, usually hidden in the sand (during the day and in the dry season).

Status and conservation: ***Ichnusomunda sacchii*** is known only from the sandy dunes of Is Arenas. Despite intensive research along the Sardinian coasts, no other population of this species has been found. In fact, in similar habitats ***I. sacchii*** is replaced by the widely distributed *Polloneriella contermina* (Pfeiffer, 1848) and sometimes by *Xerosecta dohrni* (Paulucci, 1882) to the north.

The most extensive sand dunes of the northwestern Mediterranean are found in Sardinia, but since the end of the fifties, some of these peculiar biotopes (Is Arenas, Buggerru, Marina di Gonnessa) have been altered by reforestation with pines (especially *Pinus halepensis*) in order to arrest the advance of the dunes onto farmland. Building speculators have caused further damage, currently limited to a few areas of the south coast (De Marco & Mossa, 1983).

The biotope of Riu Piscinas (no. 20/35 in the checklist


DG
E
VD
IS
OS
PR
P
12
BP
GT
PG
PN
13
14
V
OS
P
BP
GA
15
VP
CGA
GT
16
VP
OSO
17
12-13, 15-17 4 mm
14 2 mm

of the Società Botanica Italiana; no. ITB000031 of the "Nature-2000 Web") is one of the most important and least altered. The dunes stretch about a kilometer inland, achieving an altitude of about 100 m on the left bank of Riu Naracauli, where the quantity of sand is greatest. The biotope of Riu Piscinas has plant communities typical of the dunes of Sardinia, e.g., *Ammophiletum arundinaceae, Crucianelletum maritimae, Centaureo-Ononidetum ramosissimae,* and *Pistacio-Juniperetum macrocarpae*

With regard to the fauna, the coleopteran biocenosis, characterized by localized Sardinian endemics, such as *Typhoeus hiostius* Gené, 1836 (Coleoptera, Geotrupidae), *Calicnemis sardiniensis* Leo, 1895 (Coleoptera, Dinastidae), and *Thorectes sardous* Erichson, 1847 (Coleoptera, Geotrupidae) (Cassola, 1978; A. Casale, personal communication) is of considerable interest. ***I. sacchii*** is undoubtedly the most interesting and important animal species living in the biotope. Although ***I. sacchii*** is very common in this site, its limited distribution would be a clear risk factor in the face of man-made modifications to the peculiar biotope in which it lives. Hence, it can be defined as vulnerable (VU: D2; see IUCN, 1994).

DISCUSSION

The new species shows a unique combination of anatomical characters that prevents its inclusion in any other known genus of the Hygromiidae. Consequently, a new genus is necessary to accommodate it. The new genus, ***Ichnusomunda,*** is easily distinguishable from all the other hygromiid genera (Tables 2, 3).

The right ommatophore free of the genitalia and the dart-sac complex (consisting of an inner dartless stylophore and an outer dart-secreting stylophore) limits the comparison to the hygromiid genera traditionally assigned to the "Helicellinae." They include some genera with 0 + 2 DSC, e.g., *Candidula* Kobelt, 1871, *Cernuella* Schlüter, 1838 (with three subgenera: *C.* (*Cernuella*), *Xeroamanda* Monterosato, 1892, and *Xerocincta* Monterosato, 1892), *Cernuellopsis* Manganelli & Giusti, 1988, *Microxeromagna* Ortiz de Zarate Lopez, 1950, *Polloneriella* Alzona & Alzona Bisacchi, 1940, *Xeromunda* Monterosato, 1892, *Xeroplana* Monterosato, 1892, and *Xerosecta* Monterosato, 1892), and others with 2 + 2 DSC, e.g., *Helicella* Férussac, 1821, *Helicopsis* Fitzinger, 1833, *Helicotricha* Giusti et al., 1992, *Pseudoxerophila* Westerlund, 1879, *Xerolenta* Monterosato, 1892, *Xeropicta* Monterosato, 1892, *Xerotricha* Monterosato, 1892. Some of the genera with 0 + 2 DSC are thought to form monophyletic groups with others with 2 + 2 DSC: *Candidula* with *Helicella* (Hausdorf, 1988; Giusti et al., 1992), *Xeromunda* with *Pseudoxerophila* and *Xerolenta* (Hausdorf, 1988; Giusti et al., 1992), *Microxeromagna* and *Xerosecta* with *Helicotricha* (Giusti et al., 1992).

Ichnusomunda shares the pedal innervation of the penis with *Candidula* (and its sister group, the 2 + 2 DSC *Helicella*), *Cernuella, Cernuellopsis,* and *Xeroplana.* It also shares three frenula connecting the penial papilla to the penis walls with two of the three subgenera of *Cernuella, C.* (*Cernuella*) and *C.* (*Xeroamanda*). ***Ichnusomunda*** differs markedly from all of those by virtue of a completely different organization of the dart-sac complex.

Candidula (and the 2 + 2 DSC *Helicella*) has a short left lateral lobe of the pallial margin and a dart-sac complex which lies side-by-side with the vagina so that its longitudinal axis is parallel or forms a very acute angle with that of the vagina. The DSC lacks a basal portion and consists of a large bottle-shaped outer stylophore and a vestigial inner stylophore. The latter is not visible from the outside and is hardly recognizable as such even when the dart-sac complex is dissected. The stylophores open into a large tonguelike structure (for *Candidula* see Hausdorf, 1988: 15–17, figs. 10, 11 [*C. unifasciata* (Poiret, 1801) and *C. gigaxii* (Pfeiffer, 1850)]; for *Helicella* see Giusti & Manganelli, 1989: figs. 6, 7, 9C [*H. itala* (Linnaeus, 1758)]).

Cernuella differs in having a dart-sac complex which lies side-by-side with the proximal vagina so that the wall of the inner stylophore adheres to that of the vagina (the longitudinal axis of the dart-sac complex forms an acute angle with that of the vagina). The DSC lacks a basal portion and has clearly visible outer and inner stylophores of quite similar shape and size. The openings of the two stylophores are distant from each other and situated inside the groove of the dart-gun (a conical structure through which the dart is expelled) (for *Cernuella* (*Cernuella*) see Hausdorf, 1988:18, fig. 12 [*C. virgata* (Da Costa, 1778)];

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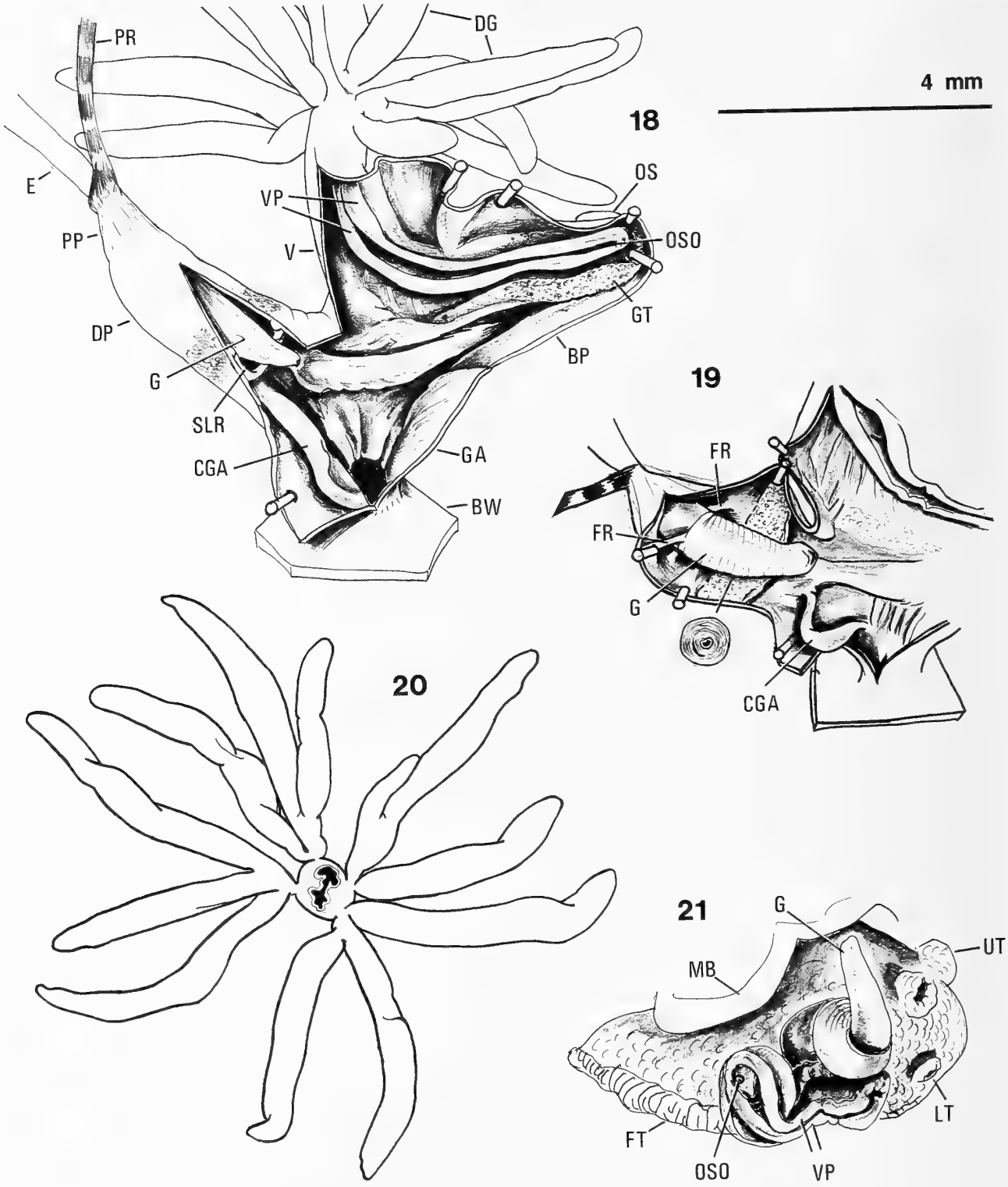
Explanation of Figures 12 to 17

Details of distal genitalia of specimens of ***Ichnusomunda sacchii*** Giusti & Manganelli, gen. & sp. nov., from Is Arenas, Cuccuru Pranu (Arbus, Cagliari, Sardinia, Italy), 32SMJ5378, G. Manganelli, L. Manganelli & G. Cappelli leg. 19 October 1995. The distal genitalia *in toto,* with penial nerve originating from pedal ganglion (12); detail of dart-sac complex with transverse section of inner stylophore (13); the dart (14); dissection of vagina and basal portion of dart-sac complex (15–17). Giusti Collection (Dipartimento di Biologia Evolutiva, Via Mattioli 4, I-53100 Siena, Italy). Key: BP, basal portion of dart-sac complex; CGA, crestlike structure of genital atrium; DG, digitiform glands; E, epiphallus; GA, genital atrium; GT, glandular tissue; IS, inner stylophore; OS, outer stylophore; OSO, outer stylophore opening; P, penis; PG, pedal ganglion; PN, penial nerve; PR, penial retractor muscle; V, vagina; VD, vas deferens; VP, vaginal pleats.


PR
DG
4 mm
18
E
VP
OS
PP
V
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GT
DP
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G
SLR
CGA
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BW
19
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FR
G
CGA
20
21
G
UT
MB
LT
FT
OSO
VP

Manganelli & Giusti, 1988: 345–346, figs. 4A–G, 5A–F, 14A, B [*C. virgata* and *C. cisalpina* (Rossmässler, 1837)]); for *Cernuella* (*Xeroamanda*) see Manganelli & Giusti, 1988: fig. 6A–E [*C. caruanae* Kobelt (1888)]; Manganelli et al. 1996: figs. 5–9 [*C. amanda* Rossmässler, (1838)]; for *Cernuella* (*Xerocincta*) see Manganelli & Giusti, 1988:348, 350, figs. 7A–H, 14C [*C. neglecta* (Draparnaud, 1985)].)

Cernuellopsis differs in having a short left lateral lobe of the pallial margin and a dart-sac complex that lacks a basal portion and is also asymmetrically disposed with respect to the vagina. The proximal vagina terminates, forming an acute angle with the DSC, on the side of the inner stylophore facing the outer stylophore (not between the two stylophores: it is not possible to section the dart-sac complex and vagina into two specular halves). *Cernuellopsis* also differs from ***Ichnusomunda*** in the internal structure of the dart-sac complex and vagina. It has a cylindrical "dart-gun," with an open base (that facing the proximal vagina) and an apex (that facing genital atrium) that extends into a short, conical tube. It has a pleat that extends from the inner walls of the proximal vagina to the dart-sac area, where it branches, giving rise to a pleat that penetrates the lumen of the "dart-gun" on one side and to a tonguelike structure that widens to laterally embrace the "dart-gun" cylindrical structure on the other side. The openings of the two stylophores (visible only after dissection of the cylindrical structure) are distinct and not far from each other (that of the outer stylophore is closer to the apex of the dart-gun) (for the only known species of *Cernuellopsis, C. ghisottii* see Manganelli & Giusti, 1988:334–336, 338, figs. 1A–G, 2A–E, 14L)

Xeroplana differs in having a dart-sac complex that lies side-by-side with the proximal vagina so that the wall of the inner stylophore adheres to that of the vagina (the longitudinal axis of the dart-sac complex forms an acute angle with that of the vagina). The DSC lacks a basal portion and has well-formed outer and inner stylophores of quite similar shape and size. The dart-sac complex contains a small "dart-gun" that projects into the distal vagina; the dart-gun is similar in shape, but smaller than that of *Cernuella* and is open to the tip. The openings of the two stylophores are independent, one (that of the inner stylophore) before the other, both inside the groove of the dart-gun. The dart is peculiar with respect to those of the other genera: it has only one lateral wing that arises at one-third of its length and ends at the tip (in transverse section near tip it is polygonal, with a lateral, hooklike projection) (for *Xeroplana* see Manganelli & Giusti, 1988: figs. 12A–E, 14D [*X. doumeti* (Bourguignat, 1876), as *X. lacosteana* (Morlet, 1881)]; Manganelli et al., 1997: figs. 4–12 [*X. idia* (Issel, 1885)]).

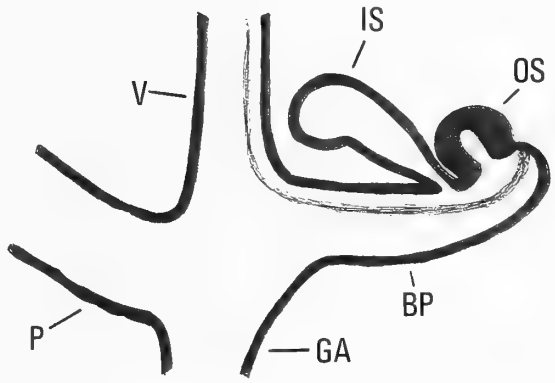

Figure 22

Scheme of dart-sac complex of ***Ichnusomunda sacchii*** Giusti & Manganelli, gen. & sp. nov. Key: BP, basal portion of dart-sac complex; GA, genital atrium; IS, inner stylophore; OS, outer stylophore; P penis; V, vagina.

Unlike the genera discussed above, which share pedal innervation of the penis with ***Ichnusomunda,*** certain other genera, e.g., *Xeromunda* and the 2 + 2 DSC *Xerolenta* and *Pseudoxerophila,* share a basal portion connecting the stylophores to the vagina with ***Ichnusomunda.*** It also shares a similar inner stylophore structure with *Pseudoxerophila* and one species of *Xeromunda* (*X. peloponnesia* Hausdorf, 1990).

Xeromunda, Xerolenta, and *Pseudoxerophila* differ from ***Ichnusomunda*** by virtue of cerebral innervation of the penis and other characters. In particular, *Xeromunda* differs from ***Ichnusomunda*** in that it has a short left lateral lobe of the pallial margin, a long proximal penis (about half of whole penis length), no frenula connecting

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Explanation of Figures 18 to 21

Details of distal genitalia of specimens of ***Ichnusomunda sacchii*** Giusti & Manganelli, gen. & sp. nov., from Is Arenas, Cuccuru Pranu (Arbus, Cagliari, Sardinia, Italy), 32SMJ5378, G. Manganelli, L. Manganelli & G. Cappelli leg. 19 October 1995. Dissection of penis to show penial papilla (18, 19); the digitiform glands (20); during copula distal parts (penis, basal portion of dart-sac complex and genital atrium) are extroflected from genital opening (21). Giusti Collection (Dipartimento di Biologia Evolutiva, Via Mattioli 4, I-53100 Siena, Italy). Key: BP, basal portion of dart-sac complex; BW, body wall; CGA, crestlike structure of genital atrium; DG, digitiform glands; DP, distal penis; E, epiphallus; FR, frenulum; FT, foot; G, penial papilla; GA, genital atrium; GT glandular tissue; LT, lower tentacle; MB, mantle border; OS, outer stylophore; OSO, outer stylophore opening; PP, proximal penis; PR, penial retractor muscle; SLR, sphincterlike ring; UT, upper tentacle; V, vagina; VP, vaginal pleats.

Table 1

Nominal taxa of the species group introduced for Sardinian xerophilous hygromiids.

X[erophila]. balteata Pollonera, 1892:4–5.

Type material: 3 syntypes (MRSNT 149), one of which selected as lectotype (Figure 23).
Type locality: "Tudu Mannu presso Cagliari [Tudu Mannu near Cagliari] (Camerano)."
Status: a nominal species of *C.* (*Cernuella*) in need of revision.

Helix Dohrni Paulucci, 1882:252–253, 1883: pl. 7, figs. 3, 3a, b.

Type material: 2 syntypes (MZUF 10820, 13121), one of which selected as lectotype (Figure 26).
Type locality: "Habitat prope Sassari."
Status: *Xerosecta dohrni* (Paulucci, 1882) see Manganelli et al. (1995).

Helix Hillyeriana Paulucci, 1882:251–252, 1883: pl. 7, fig. 4, 4a–d.

Type material: In Paulucci collection there are three lots of *Helix hillyeriana* (11503 + 13122, 11504, 11505). One contains a juvenile specimen (11505), another a specimen assigned to a "forma *minor*" (11504), and the last (11503 + 13122) three adult shells, one of which (11503) is figured by Paulucci (1883). This specimen (11503) is designated as the lectotype (Figure 25).
Type locality: "Habitat in locu Decimomannu dicto, insulae Sardiniae."
Status: *Xerosecta hillyeriana* (Paulucci, 1882) see Manganelli et al. (1995).

Helix parva Pfeiffer, 1848:441–442.

Type material: no syntypes are known. In the Forschungsinstitut und Naturmuseum Senckenberg (Frankfurt a.M., Germany) there is a lot of four specimens (SMF 10224), which could have been presented by L. Pfeiffer. One of these (Figure 27) is figured by Kobelt (1878: pl. 152, fig. 1548).
Type locality: "in Sardinien."
Status: a nominal species of *C.* (*Cernuella*) in need of revision.

Helix tuta Paulucci, 1882:245–248, 1883: pl. 7, figs. 1, 1a, b.

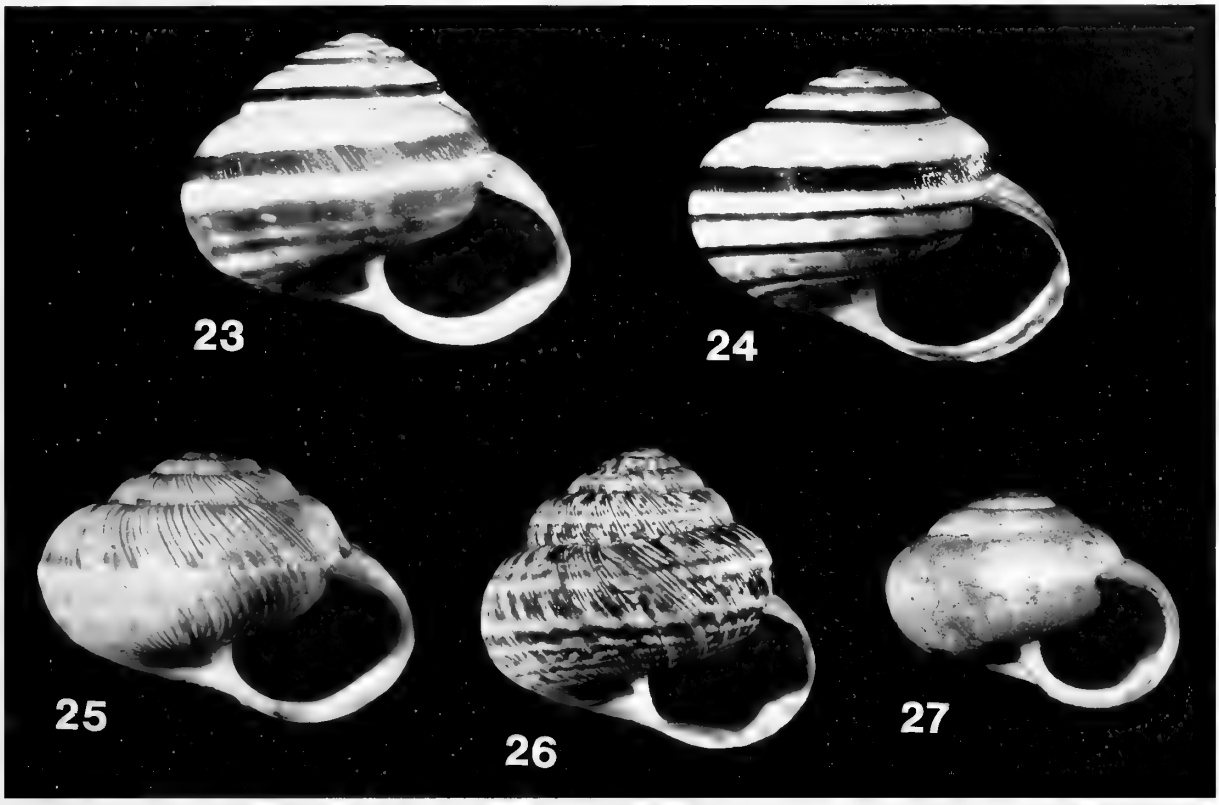
Type material: In Paulucci Collection there are many lots of *Helix tuta*: four from Selinunte (Sicily) (MZUF 11506, 11518, 11519, 11520), one from "anfiteatro di Cagliari" (MZUF 11517), the others from "i monti tra Sarroch e S. Pietro di Pula nella provincia di Cagliari" (MZUF, 11507, 1508, 11509 + 13120, 11510, 11511, 11512, 11513, 11514, 11515, 11516). All of the latter, except 11509, are assigned to distinct forms eg., *minor zonata* (11507), *minor* (11508, 11517), *zonata* (11510), *minima* (11511), *elata* (11512), *elata zonata* (11513), *minima zonata* (11514), *minor pallescens* (11515), and *pallescens* (11516). One (11509) of the eight specimens of 11509 + 13120 corresponding to that figured by Paulucci (1883), is selected as the lectotype (Figure 24).
Type locality: "Abita sui monti tra Sarroch e S. Pietro di Pula nella provincia di Cagliari e l'anfiteatro della città omonima. La conosco pure di Sicilia ed i miei esemplari di questa provenienza mi vennero donati dal professor Hillyer Giglioli il quale li aveva raccolti presso Selinunto [It lives in the mountains between Sarroch and S. Pietro di Pula in the province of Cagliari and the amphitheatre of this town. I know it from Sicily; the Sicilian specimens were given to me by professor Hillyer Giglioli who collected them near Selinunto]." Following the designation of the lectotype the type locality is restricted to "monti tra Sarroch e S. Pietro di Pula nella provincia di Cagliari."
Status: a nominal species of *C.* (*Cernuella*) in need of revision.

the base of the penial papilla to the penis wall, a severely degenerated inner stylophore (except in *X. peloponnesia*) represented by a large cavity around the upper part of the basal portion and the vagina. Moreover, the species of *Xeromunda,* except *X. thessalica* Hausdorf, 1990, have only two tufts of digitiform glands on one side of the vagina. Other species, e.g., *X. peloponnesia* and *X. vulgarissima* (Mousson, 1859), also have a long flagellum (length of epiphallus plus penis) (for *Xeromunda* see Figure 28 [*X.* cf. *durieui* (Pfeiffer, 1848)], Figure 29 [*X. peloponnesia*], and Hausdorf, 1988:figs. 18, 19 [*X. candiota* (Pfeiffer, 1848)], Manganelli & Giusti, 1989: figs. 1A–F, 2A–L, 3E, 5B [*X.* cf. *durieui*], figs. 3A–D, 4A–F [*X. candiota*], Hausdorf, 1990: figs. 1–3 [*X. candiota*], figs. 4–6 [*X. peloponnesia*], figs. 7–10 [*X. vulgarissimal*], figs. 12–14 [*X. thessalica*]; for *Xerolenta* see Hausdorf, 1988: 22, 23, fig. 17 [*X. obvia* (Menke, 1828)]).

Pseudoxerophila deserves special attention because, besides the basal portion, it shares a similar inner stylophore structure, i.e., long, slender, with thin walls and wide lumen, bent to adhere to the upper side of the basal portion, with ***Ichnusomunda*** (and *X. peloponnesia* the taxonomic status of which needs to be reconsidered). *Pseudoxerophila* and ***Ichnusomunda*** also share a very short proximal penis and a long left lateral lobe of the pallial margin. Again *Pseudoxerophila* differs from ***Ichnusomunda*** in having cerebral innervation of the penis and 2 + 2 dart-sac complex (for the only known species of *Pseudoxerophila, P. bathytera* (Westerlund & Blanc, 1879), see Figure 30 and Hausdorf, 1989:20–22, figs. 14–16).

Before concluding, a note about *Polloneriella* is warranted. This taxon has recently been proposed as a subgenus of *Xerosecta* (Manganelli & Giusti, 1988). The only species of *Polloneriella, P. contermina* (Pfeiffer, 1848), has genitalia that are quite characteristic with respect to those of the typical subgenus (re-examination of its rank and relationships is necessary), particularly by the fact that the two stylophores are inside a bilobe swelling of the vagina walls that somewhat imitates the basal portion of the dart-sac complex in ***Ichnusomunda.*** Nevertheless, they are quite unrelated: apart from the cerebral innervation of its penis, *Polloneriella* is easily distinguished by an inner stylophore slightly smaller than the outer and clearly evident, situated side-by-side with the outer (its longitudinal axis is parallel to that of the outer); the peculiar shape of the dart; a penial papilla without frenula, and with a different transverse section (for the only known species of *Polloneriella, P. contermina* (Pfeiffer, 1848) see Manganelli & Giusti, 1988:354, figs. 10A–E, 14G).

The remaining genera have no significant characters in common with ***Ichnusomunda,*** apart from the dart-sac complex and the right ommatophore free of the genitalia (*Helicopsis, Helicotricha, Xeropicta,* and *Xerotricha*), the 0 + 2 DSC (*Microxeromagna*), and the very short prox-



Explanation of Figures 23 to 27

Type and historical specimens of nominal taxa of the species group introduced for Sardinian xerophilous hygromiids. Lectotype of *Xerophila balteata* Pollonera, 1892 from "Tudu Mannu presso Cagliari," Pollonera collection, Museo Regionale di Scienze Naturale (Turin, Italy) MRSNT no. 149/A. Lectotype of *Helix tuta* Paulucci, 1882 from "Monti tra Sarroch e S. Pietro di Pula," Paulucci collection, Museo di Zoologia dell'Università di Firenze (Florence, Italy), MZUF no. 11509. Lectotype of *Helix hillyeriana* Paulucci, 1882 from "Decimomannu," Paulucci collection, Museo di Zoologia dell'Università di Firenze (Florence, Italy), MZUF no. 11503. Lectotype of *Helix dohrni* Paulucci, 1882 from "Sassari," Paulucci collection, Museo di Zoologia dell'Università di Firenze (Florence, Italy), MZUF no. 10820. Shell of *Helix parva* Pfeiffer, 1848, figured by Kobelt (1878: pl. 103, fig. 1548), Forschungsinstitut und Naturmuseum Senckenberg (Frankfurt A. M., Germany), SMF no 10224. All ×4.

imal penis (*Xerosecta*). Consequently, they will not be further discussed (for *Helicopsis* see Giusti & Manganelli, 1989 and Giusti et al., 1992; for *Helicotricha* see Giusti et al., 1992; for *Xeropicta* see Schileyko, 1978; for *Xerotricha* see Giusti & Manganelli, 1989; for *Microxeromagna* see Manganelli & Giusti, 1988; for *Xerosecta* see Manganelli & Giusti, 1988 and Manganelli & Favilli, 1996).

From the above discussion it is evident that ***Ichnusomunda*** shares anatomical character-states with two separate groups of helicelline hygromiids (i.e., *Cernuella* and its allies vs. *Xeromunda, Xerolenta,* and *Pseudoxerophila*). This may occur in three ways. ***Ichnusomunda*** may share a set of character-states with *Cernuella* through common ancestry and another set with *Xeromunda, Xerolenta,* and *Pseudoxerophila* through homoplasy; or it may share a set of character-states with *Xeromunda, Xerolenta,* and *Pseudoxerophila* through common ancestry, and another set with *Cernuella* through homoplasy; or it may share both sets of character-states with *Cernuella* and *Pseudoxerophila-Xerolenta-Xeromunda* through common ancestry (i.e., as plesiomorphic states with respect to the larger group that contains all three groups of taxa) without any homoplasy. The only way to choose between these three possibilities is to have a phylogenetic hypothesis based on other characters. We regard these character-states (pedal innervation of penis, long left lateral lobe of pallial margin, frenula in penial papilla, basal portion of dart-sac complex, and inner stylophore of ***Ichnusomunda***-type) as apomorphic which means that the anatomy of ***Ichnusomunda*** is subject to homoplasy. We derived this interpretation from the fact that all the possible sister groups of the larger group containing the three groups of taxa (whatever they are: hygromiids or even another, larger helicoid group) never have these character-states, which only appear in the hygromiid genera cited.

Table 2

List of the main characters used in the discussion of the relationships of ***Ichnusomunda.***

1—Penial nerve

Penial nerve from right cerebral ganglion = A
Penial nerve from right pedal ganglion = B

2—Left lateral lobe

Left lateral lobe short (the distance between the upper vertex of LLL and the lower of LDL is equal to or greater than the length of LLL) = A
Left lateral lobe medium- to long (the distance between the upper vertex of LLL and the lower of LDL is very short) = B

3—Dart-sac complex (number of stylophores forming the DSC on opposite side of vagina)

Dart-sac complex 0 + 2 = A
Dart-sac complex 2 + 2 = B

4—Vagina and dart-sac complex

Dart-sac complex symmetrically disposed with respect to vagina (it is possible to divide the dart-sac complex and vagina longitudinally into two specular halves) = A
Dart-sac complex asymmetrically disposed with respect to vagina (it is not possible to divide the dart-sac complex and vagina longitudinally into two specular halves) = B

5—Basal portion of dart-sac complex

Dart-sac complex without basal portion = A
Dart-sac complex with out basal portion, but with two stylophores sunk between two large vaginal swellings = B
Dart-sac complex with cylindrical, more or less developed basal portion joined perpendicularly to distal vagina = C

6—Shape and size of inner stylophore

Inner stylophore saclike but very elongated (Schileyko, 1978: fig. 245) = A
Inner stylophore saclike, approximately same size as, or slightly smaller than, outer stylophore (Giusti & Manganelli, 1989: fig. 9D) = B
Inner stylophore of *Xerotricha*-type (inner stylophore saclike, markedly smaller than outer stylophore and with only its apical part visible from outside; Giusti & Manganelli, 1989: fig. 9A) = C
Inner stylophore of *Helicella*-type (inner stylophore vestigial, not visible from outside, reduced to form a small cavity between vagina and large, bottle-shaped outer stylophore; Giusti & Manganelli, 1989: fig. 9C) = D
Inner stylophore of ***Ichnusomunda***-type (saclike approximately same size as, or larger than, outer stylophore, more or less elongated with thin walls and large lumen and, bent to adhere to upper side of basal portion, this paper: Figure 27) = E
Inner stylophore of *Xeromunda*-type (severely degenerated, represented by a large cavity around the upper part of the basal portion and the vagina; this paper: Figure 28) = F

7—Dart-sac complex opening into vagina

Stylophore openings between two pleats not larger than other vaginal pleats = A
Stylophore openings between two large U-shaped vaginal pleats = B
Stylophore openings in the basal portion of dart-sac complex, between two large U-shaped pleats originating in proximal vagina = C
Stylophore openings in large tonguelike structure (two distinct tonguelike structures in the case of 2 + 2 DSC; Giusti & Manganelli, 1989: fig. 9A) = D
Stylophore openings in large tonguelike structure which forms a single tubelike structure in the case of 2 + 2 DSC and sometimes in the case of 0 + 2 DSC derived from 2 + 2 DSC ? (Giusti & Manganelli, 1989: figs. 9C) = E
Stylophore openings in groove of structure similar to a dart-gun, but simpler and shorter than that of other hygromiids, open as far as tip = F
Stylophore openings in groove of dart-gun, having short, closed tip = G
Stylophore openings in dart-gun, having large, closed, cylindrical muff and small tip = H

8—Dart

Cernuella-type (straight or slightly curved with rounded or polygonal section for most of length; transverse section of tip rhombic or in form of cross with two opposite arms longer than other two) = A
Microxeromagna-type (straight or slightly curved with two opposite lateral wings for most of its length and rhombic section) = B
Polloneriella-type (straight or slightly curved with one lateral wing for most of its length and rhombic section) = C
Xeroplana-type (straight or slightly curved with rhombic section and hook-like projection) = D

9—Flagellum

Flagellum short- to medium (approximately one-fourth length of the epiphallus plus penis) = A
Flagellum very long (approximately equal to length of epiphallus plus penis) = B

10—Frenula connecting penial papilla base with penial walls

No frenula = A
Three frenula = B

11—Transverse section of apical penial papilla

Cernuella-type (wall of penial papilla solid, with some small lacunae) = A
Helicopsis-type (wall of penial papilla with three lacunae all around central lumen, at least in *H. striata*) = B
Helicotricha-type (wall of penial papilla solid, with T-shaped pilaster alongside its entire length, joined to penial papilla by a peduncle) = C
Polloneriella-type (wall of penial papilla separated into peripheral and central portions by large annular lacuna) = D
Microxeromagna-type (wall of penial papilla very thin and open along one side) = E
Xerosecta-type (wall of penial papilla with pilasters and lacunae to imitate corpora cavernosa) = F

12—Appendix in the distal genitalia

absent = A
penial = B

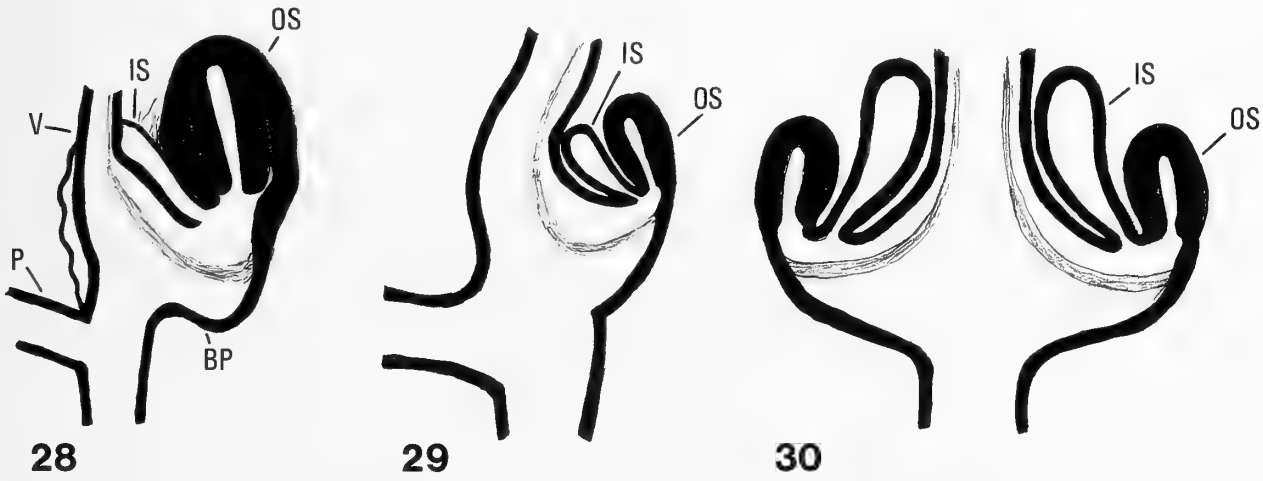
Table 3

List of taxa and main characters cited in the discussion. All the taxa listed have a right ommatophore free of the genitalia and a dart-sac complex (consisting of an inner dartless stylophore and an outer dart-secreting stylophore).

	1	2	3	4	5	6	7	8	9	10	11	12
Candidula	B	A	A	A	A	D	E	A	AB	A	A	A
C. (Cernuella)	B	B	A	A	A	B	G	A	A	B	A	A
C. (Xeroamanda)	B	B	A	A	A	B	G	A	A	B	A	A
C. (Xerocincta)	B	B	A	A	A	B	G	A	A	A	A	A
Cernuellopsis	B	A	A	B	A	B	H	A	A	A	A	A
Helicella	B	A	B	A	A	D	E	A	A	A	A	A
Helicopsis	A	A	B	A	A	B	AB	A	A	A	B	A
Helicotricha	A	A	B	A	A	B	B	A	B	A	C	A
Ichnusomunda	B	B	A	A	C	E	C	A	A	B	A	A
Microxeromagna	A	A	A	A	A	A	A	B	B	A	D	A
Polloneriella	A	A	A	A	B	B	A	C	A	A	E	A
Pseudoxerophila	A	A	B	A	C	E	B	A	B	A	A	A
Xerolenta	A	A	B	A	C	F	C	A	A	A	A	A
Xeromunda	A	A	A	A	C	F	C	A	AB	A	A	A
"Xeromunda" peloponnesia	A	A	A	A	C	E	?	A	B	A	A	A
Xeroplana	B	B	A	A	A	B	F	D	B	A	A	A
Xeropicta	?	?	B	A	A	A	?	?	A	A	?	B
Xerosecta	A	A	A	A	A	B	A	A	A	A	F	A
Xerotricha	A	A	B	A	A	C	D	A	A	A	AB	A

If the pedal penial innervation is a good character to identify monophyly of the group which includes *Candidula, Cernuellopsis, Cernuella* (*Cernuella*), *Cernuella* (*Xeroamanda*), *Cernuella* (*Xerocincta*), *Helicella,* and *Xeroplana,* then *Cernuella* (*Cernuella*) and *Cernuella* (*Xeroamanda*) are the closest to ***Ichnusomunda.*** This conclusion is supported by the fact they share at least one synapomorphy: three frenula at the base of the penial papilla. If so, a profound, autoapomorphic modification of the dart-sac complex distinguishes ***Ichnusomunda*** from *Cernuella.* This modification produced an organization of the dart-sac complex which is homoplastic for two characters (basal portion of dart-sac complex; inner stylophore of ***Ichnusomunda***-type) with respect to that in another group of taxa of the helicellids, the group including *Xeromunda, Xerolenta,* and *Pseudoxerophila.*

The alternative interpretation, the basal portion of dart-sac complex, identifying the putative monophyletic group



Explanation of Figures 28 to 30

Scheme of dart-sac complex of *Xeromunda candiota* (Pfeiffer, 1848), *X. peloponnesia* Hausdorf, 1990, and *Pseudoxerophila bathytera* (Westerlund & Blanc, 1879). Key: BP, basal portion of dart-sac complex; GA, genital atrium; IS, inner stylophore; OS, outer stylophore; P, penis; V, vagina.

Ichnusomunda-Xeromunda-Xerolenta-Pseudoxerophila, in which *Pseudoxerophila,* ***Ichnusomunda,*** and *X. peloponnesia* are more primitive due to the less derived structure of the inner stylophore) obviously implies that the pedal penial innervation, the long left lateral lobe of pallial margin and the penial papilla with three basal frenula of ***Ichnusomunda*** are of a homoplastic nature.

Anatomical research for future cladistic analysis is currently underway on the different taxa of the genus group of the hygromiids. Until the results of this research are available, the first interpretation seems more probable on the basis of the characters involved (pedal innervation of penis, long left lateral lobe of pallial border, and penial papilla with three frenula) and biogeographical data (*Xeromunda, Xerolenta,* and *Psedoxerophila* have a prevalent E-Mediterranean distribution; *Cernuella* and the new species are prevalently W-Mediterranean).

Irrespective of this tentative conclusion, the genital structure of ***Ichnusomunda*** shows a clear case of homoplasy. The case, certainly not unique in the hygromiids or in the helicoids in general, suggests prudence in the common practice of inferring phylogeny and splitting taxa above the genus level on the basis of genital characters.

ACKNOWLEDGMENTS

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THE VELIGER

Periwinkle's Progress: The Atlantic Snail *Littorina saxatilis* (Mollusca: Gastropoda) Establishes a Colony on a Pacific Shore

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Abstract. The common ovoviviparous and eurytopic Atlantic Ocean periwinkle *Littorina* (*Neritrema*) *saxatilis* (Olivi, 1792) has established reproducing populations in San Francisco Bay, California, USA. The first population was discovered in 1993. The probable mechanism of introduction into the Bay is the disposal of seaweeds (the brown algae *Ascophyllum nodosum* and *Fucus vesiculosus*) used as transport packing with polychaete worms used for fish bait. These worms, seaweed, and associated periwinkles originate from Maine. An alternative mechanism may be the similar disposal of seaweeds used as packing for imported Atlantic lobsters (*Homarus americanus*) for the restaurant trade. *Littorina saxatilis* could occupy a range on the Pacific American coast from Baja California to western Alaska, and as such it would come into direct contact with the consubgeneric *Littorina* (*Neritrema*) *subrotundata* (Carpenter, 1864) (synonym: *Littorina newcombiana* Hemphill, 1877) and *Littorina* (*Neritrema*) *sitkana* Philippi, 1846, which occur from southern Oregon and north. These latter two species occur in a range of morphological-physiological ecotypes that are closely analogous to those of *Littorina saxatilis*. Eradication of this snail invasion may be possible because the populations are easily accessed and relatively small. However, no tested eradication methods are known, nor are jurisdictional authority or regulatory issues clear relative to initiating potential removal of this species.

INTRODUCTION

The common Atlantic Ocean rough periwinkle *Littorina* (*Neritrema*) *saxatilis* (Olivi, 1792) occurs in North America from Chesapeake Bay north to the high boreal and subarctic waters of Hudson Bay, Baffin Island, Greenland and the Barents Sea, and south along the European coast to the Straits of Gibraltar (Reid, 1996). Outlying populations which occur at the Azores and Canary Islands, at the north end of the Adriatic Sea and at Tunisia in the Mediterranean Sea, and at three sites in the South Atlantic Ocean in Namibia and South Africa, may represent relicts of formerly more widespread populations, transport by migrating birds, or introductions through human activities (Reid, 1996; McQuaid, 1996a). We here report on the introduction and establishment of *Littorina saxatilis* in the Pacific Ocean.

DISCOVERY AND DESCRIPTION OF HABITAT

On 4 October 1993 we discovered a population of *Littorina saxatilis* living intertidally on scattered large rocks (placed here for shoreline stabilization) in the high intertidal zone at a site on the eastern shore of San Francisco Bay, California. This site is adjacent to the Emeryville Marina Launching Facility, a public dock and boat ramp in the city of Emeryville. Subsequent collections from 1993 to 1996 (Table 1) revealed a reproducing and well-established population, with numerous snails occupying crevices and empty barnacle shells. One quantitative sample taken in November 1996 indicated a density of over 1800 snails per square meter (Table 1).

Other species found on and under these same rocks are the native barnacle *Balanus glandula* Darwin, 1854, the native snail *Assiminea californica* (Tryon, 1865), the native isopod *Ligia occidentalis* Dana, 1853, the native crabs *Pachygrapsus crassipes* Randall, 1839, and *Hemigrapsus oregonensis* (Dana, 1851), the Atlantic bryozoan *Bowerbankia gracilis* Leidy, 1855, the Japanese sea anemone *Diadumene lineata* (Verrill, 1873) [synonym: *Haliplanella luciae* (Verrill, 1898)], and the cryptogenic (neither clearly introduced nor native; Carlton, 1996) green algae *Enteromorpha* sp. and *Ulva* sp. In 1993 we found native periwinkles of the *Littorina scutulata* Gould, 1849—*Littorina plena* Gould, 1849, complex on these rocks along with *Littorina saxatilis*. However, in November 1996 no native periwinkles occurred where *L. saxatilis* was found; rather, the native species was found only on rocks commencing about 5 m to the

Table 1

Records of *Littorina saxatilis* in San Francisco Bay.

Date	Search area; search effort (p = person; VT = vertical transects)	Number (height) collector (See lettered footnotes)
	Emeryville Marina, Emeryville	
07 Oct 93	2 m × 5 m; 1 p × 60 min	73 (1–10 mm)[a]
28 Feb 94	2 m × 10 m; 2 p × 30 min	26 (3–10 mm)[b]
22 Jul 94	2 m × 10 m; 4 p × 15 min	3 —[c]
21 Feb 95	2 m × 5 m; 1 p × 30 min	1 (3 mm)[a]
21 Apr 95	2 m × 5 m; 1 p × 30 min	2 (5–9 mm)[a]
27 Apr 95	2 m × 5 m; 1 p × 20 min	1 (10 mm)[a]
19 May 95	2 m × 5 m; 2 p × 20 min	3 (6–8 mm)[d]
20 Jun 95	2 m × 5 m; 1 p × 90 min	14 (3–8 mm)[a]
18 Oct 95	2 m × 10 m; 2 p × 45 min	9 (4–10 mm)[e]
04 Nov 95	7 VT (@ 3 m × 0.6 m); 1 p × 70 min	22* (to 11 mm)[f]
25 Jan 96	7 VT (@ 3 m × 0.6 m); 1 p × 70 min	28* (to 11 mm)[f]
24 Apr 96	7 VT (@ 3 m × 0.6 m); 1 p × 70 min	24* (to 12 mm)[f]
02 May 96	2 m × 5 m; 1 p × 10 min	10* —[a]
24 Nov 96	1 m × 1.5 m; 1 p × 30 min	78 (2–12 mm)[g]
24 Nov 96	12 cm × 14.5 cm area scraped clear (=20 cc barnacle biomass)	32 (1–4 mm, and one 9 mm)[g]
	Coast Guard Island, Oakland	
28 May 96	2 m × 15 m; 2 p × 20 min	11 (3–10 mm)[b]
05 Nov 96	5 m × 45 m; 27 p × 15 min	51 (0.5–9 mm)[h]
05 Nov 96	5 m × 20 m; 3 p × 5 min	16 (4–10 mm)[i]

* Specimens not collected.

Collectors: [a] Andrew N. Cohen (ANC). [b] James T. Carlton (JTC) and ANC. [c] JTC, ANC, John Chapman, and Sarah Cohen. [d] ANC and Jonathan Geller. [e] ANC and Jeanne Yamauchi (JY). [f] JY. [g] JTC. [h] The fall 1996 class and faculty of the Williams College–Mystic Seaport Maritime Studies Program (students Laurel Bastone, Alicyn Campbell, Nicole Dobroski, Antonia Fairbanks, Hillary Frey, Dan Garner, Todd Hunter, Eileen McCullough, Emily Morland, Jan Sarra, Joshua Shapiro, Clarissa Shen, Kate Simmons, Tristan Smith, Jessica Stevens, Joe Street, Kristin Sutherland, Ben Tassinari, Andy Tolonen, Darylanne Villard, Kate Wearn, Kyra Williams, Rob Wittenmyer, and faculty members Fred Dalzell, Glenn Gordinier, Mary K. Bercaw Edwards, and James McKenna). [i] JTC, Anna Fitzgerald, and Lenny Bellet.

west of the *L. saxatilis* populations. Also occurring abundantly with *Littorina saxatilis* at this site in November 1996 was the introduced isopod *Sphaeroma walkeri* Stebbing, 1905.

We searched similar habitats in other areas of the Emeryville Marina and found no other populations of *Littorina saxatilis.* J. Yamauchi (personal communication, 1996) sampled vertical transects along 30 m of shore at this site from November 1995 to April 1996 (Table 1) and found the population to be restricted to 10 m of shore adjacent to the boat dock, as had we earlier.

On 28 May 1996 we found a second population 9 km south of Emeryville on scattered small to medium-sized rocks set in mud, in the mid to high intertidal zone of the Taney Marina beach on Coast Guard Island, Oakland, in the Oakland Estuary on the eastern side of San Francisco Bay (Table 1). The size range collected indicates reproduction at this site. The snails occur on and among the barnacle *Balanus glandula.* As with the Emeryville site, collections here in November 1996 did not include any native *Littorina.*

DESCRIPTION OF POPULATION

Littorina saxatilis shells (size range 1.0–12.0 mm) and animals at both San Francisco Bay sites conform closely with descriptions by Reid (1996). San Francisco Bay shells often have a pale yellow body whorl, occasionally with brown spots or revolving brown stripes and thus conform morphologically with the southern (low boreal Atlantic Ocean, rather than high boreal to subarctic) geographic variety *typica* (Reid, 1996).

Littorina saxatilis is easily distinguished from the native *Littorina scutulata/Littorina plena* in San Francisco Bay by its round, yellow shell. *Littorina scutulata/Littorina plena* shells are conical, and while they may be dotted or checkered, are not yellow. *Littorina keenae,* another native periwinkle in the San Francisco Bay area, possesses a distinctive flat and polished columella (inner lip).

San Francisco Bay *L. saxatilis* are heavily infected with a marine fungus (presumably *Pharcidia balani* (Winter) Bauch, 1936 [see Lindberg, 1977]) that also infests native littorines and barnacles. A subsample of 62 *L. saxatilis*

(size range 3.7–12.0 mm) collected at the Emeryville site on 24 November 1996 was 95% infected (n = 59). The more infected specimens show extensive surface decalcification and pitting when viewed microscopically. Heavy infestations, consisting of numerous pits filled with black fruiting bodies, turn the shell dark; new shell growth on the same individuals is yellow in color. Some snails have, in addition, a bright green unicellular alga on the upper body whorls.

Reid (1996) summarized the literature on the development of this periwinkle, which is the only ovoviviparous *Littorina* on the Pacific coast of North America (Behrens Yamada, 1992; Reid, 1996). Three Emeryville females collected on 24 November 1996 were dissected and found to contain embryos ranging from undifferentiated eggs to shelled snails about 0.5 mm in size: a 4 mm snail contained 18 embryos (14 of which were shelled); two 9 mm snails contained 135 embryos (95 shelled) and 194 embryos (125 shelled).

Voucher specimens of *Littorina saxatilis* from San Francisco Bay have been deposited at the California Academy of Sciences, San Francisco (catalogue number CASIZ 113210) and at the Natural History Museum, London, England (BMNH Reg. No. 1996149).

MECHANISM OF INTRODUCTION

Either of the *Littorina saxatilis* populations in San Francisco Bay could have been derived from the other, or they could each be the result of independent inoculations. In either case it seems likely that the initial inoculation(s) into the Bay were the result of anglers discarding the Atlantic brown algae *Ascophyllum nodosum* (Linnaeus) Le Jolis, 1829, which is used as packing material for live marine baitworms shipped from southern Maine (Carlton, 1992; Cohen et al., unpublished observations). *Littorina saxatilis* is common on *Ascophyllum* in New England (JTC, personal observations), and it has been found alive in boxes of *Ascophyllum*-packed worms from bait shops in the San Francisco Bay area (W. Lau, personal communication, 1995; Cohen et al., unpublished observations) and Newport Bay (Carlton, 1992). The two populations found in San Francisco Bay are adjacent to a public dock and boat ramp and to a small boat marina, and thus are likely sites for the discarding of unused bait and the bait's seaweed packing at the end of a day of fishing. We suggest that similar sites in temperate climate regions that import marine baitworms from New England would bear searches for *Littorina saxatilis* as well as the other snail species noted herein.

An alternative and closely related introduction mechanism may be seaweeds, including *Ascophyllum,* that are used as packing material for imported Atlantic lobsters (*Homarus americanus* H. Milne Edwards, 1837) in the restaurant trade and then occasionally discarded into San Francisco Bay (Miller, 1969). The Coast Guard Island site is adjacent to an officers' club where meals are served. In 1993 we found the empty shells of the edible New Zealand green-lip mussel *Perna canaliculus* (Gmelin, 1791) in the intertidal zone below the club. This mussel is sold alive in San Francisco Bay area markets. The presence of these discarded shells suggests that other seafood-associated debris—such as the seaweed packing for lobsters—may be discarded into the Bay at this site.

Molecular genetic comparisons of the San Francisco Bay populations with Atlantic populations would provide evidence for or against an introduction via baitworms or lobsters imported from New England. Berger (1973) has shown that *Littorina saxatilis* demonstrates distinct gene pool differentiation along the Atlantic coast, as would be expected from an ovoviviparous species, making subpopulations recognizable. Genetic characterization of these two populations would further provide data by which to assess potential founder effects and thus to provide a basis against which to measure future genetic changes. Of particular interest here will be comparisons of the role of local population extinction and population bottlenecks (in terms of colonization ability) as observed on occasion in Swedish *Littorina saxatilis* populations (Johanneson & Johanneson, 1995), and of the role of founder effects (in terms of the resulting levels of genetic variation) as observed in other distant and isolated populations of *Littorina saxatilis* (such as in South Africa, where populations are highly inbred [Knight et al., 1987]; see also Johanneson, 1988).

POTENTIAL GEOGRAPHIC DISTRIBUTION AND HABITAT BREADTH

The latitudinal range of *Littorina saxatilis* in the Atlantic Ocean suggests a potential range in the northeastern Pacific Ocean from Baja California to western Alaska. However, since *L. saxatilis* is ovoviviparous, natural dispersal is likely to be slow. It has been estimated that *Littorina saxatilis* may colonize new habitats within a range of about 1 km or less in about 2–10 yr (references in Reid, 1996). Reid (1996) notes that natural dispersal might be accomplished by adults being rolled along the bottom by currents or by the occasional release of encapsulated embryos, but the likeliest method is probably by transport on drifting algae. One of us (JTC) observed on rare occasions living *Littorina saxatilis* up to 5 mm in height on floating brown algae (*Ascophyllum nodosum* and *Fucus vesiculosus*) 160 km offshore of the coast of Maine. Ingolfsson (1995) also found *Littorina saxatilis* to be uncommon on floating brown algae in nearshore waters of Iceland; specimens ranged from about 3 to 10 mm in height (A. Ingolfsson, University of Iceland, personal communication, 1996).

It is difficult to predict whether *Littorina saxatilis* will spread naturally out of San Francisco Bay; several other nonindigenous species with apparently greater dispersal

abilities remain restricted to the bay decades after their establishment (Cohen & Carlton, 1995, Appendix 4). However, while ovovivipary may restrict the potential of *Littorina saxatilis* for short distance dispersal, it has been argued that it may provide an advantage over longer distances (Johannesson, 1988; Reid, 1996). The nonplanktonic young resulting from the introduction of even a single fertilized female might be more likely to produce the critical adult population density needed for successful reproduction and establishment than would the introduction of a large number of planktonic larvae. Indeed, such may have been the case in the founding of these new populations in San Francisco Bay.

Littorina saxatilis has the greatest habitat range of all *Littorina* species, which Reid (1996) related to its ovoviviparity. In the Atlantic Ocean *Littorina saxatilis* occurs intertidally on highly exposed coasts on hard substrates (where it may be restricted to sheltered microhabitats such as crevices), intertidally on moderately exposed coasts, and intertidally or subtidally in protected lagoons or estuaries, where it may also attach to submerged vegetation (Reid, 1996; McQuaid, 1996b). It occurs in salt marshes on stems of the cordgrass *Spartina* and on firm mud, and on beaches on scattered stones, shells, and debris. It is tolerant of brackish conditions, surviving salinities of 5 to 7 parts per thousand. In favorable habitats population densities may range in the 1000s, and sometimes the 100,000s, per square meter (Reid, 1996).

ECOLOGICAL IMPACT OF *LITTORINA SAXATILIS*

The establishment of *Littorina saxatilis* in San Francisco Bay raises the question of what role this snail will play as predator, prey, parasite host, or competitor, and as a new hermit crab shell resource.

In the North Atlantic Ocean, *Littorina saxatilis* is an abundant non-selective grazer on diatoms, cyanobacteria (bluegreen algae), and filamentous green and red algae (literature summarized in Reid, 1996). *Littorina saxatilis* also consumes newly settled barnacles on high intertidal rocky shores in Massachusetts and Connecticut (J. T. Carlton, personal observations). In November 1996, fecal pellets of *L. saxatilis* at the Emeryville site (two samples of 10 combined, 1.0 mm fecal pellets crushed and examined under the compound microscope, and 35 additional pellets examined individually) contained algal cells, diatoms, numerous bacteria-sized particles, crustacean fragments, and many rock grains. Individual pellets contained similar items, as well as a chironomid fly larva (Diptera), a mite (Acarina), and a rotifer (Rotifera).

Littorina saxatilis in San Francisco Bay will likely provide a ready food item for both introduced and native crabs as it does in New England (J. T. Carlton, field observations). Both in New England and elsewhere in its Atlantic range, *Littorina saxatilis* is a common prey of the European green crab *Carcinus maenas* (Linnaeus, 1758), a crab which was first found in San Francisco Bay in 1989–1990 (Cohen et al., 1995). It will be of interest to observe whether the prey handling and selection activities of *Carcinus maenas,* and elicitation of predator-response reactions, differ between *Littorina saxatilis,* with which it evolved, and the native Pacific Coast littorines, which it has never before encountered. The converse applies to native Pacific coast crabs.

Several specimens of *Littorina saxatilis* from both the Emeryville and Coast Guard Island populations show evidence of crab attacks, very likely produced by the native crabs *Hemigrapsus oregonensis* or *Pachygrapsus crassipes.* A total of four shells from 1993, 1995, and 1996 Emeryville collections show evidence of previous attack (breakage) scars (a V- or U-shaped notch in an earlier and now repaired apertural edge [outer lip], as illustrated by Raffaelli [1978]). A total of four specimens from 1993, 1994, and 1996 Emeryville collections and a total of five specimens from 1996 Coast Guard collections show evidence of fresh crab attacks, with the body whorl of the shell being torn back and around in a "can opener" fashion. Shells as small as 3.0 and 4.5 mm were attacked. A snail 6.0 mm in height from Emeryville (24 November 1996) that had been newly attacked had the shell body whorl torn back, leaving much of the animal exposed but still alive.

Competitive interactions that may occur between *Littorina saxatilis* and native periwinkles on the Pacific Coast remain to be studied. In this regard, particular focus could be given to the potential interactions between *Littorina saxatilis* and closely related species in the subgenus *Neritrema* (D. G. Reid, personal communication, 1997). While the native littorines (*L. scutulata/L. plena* and *L. keenae*) in San Francisco Bay are in the subgenera *Littorina* and *Planilittorina,* respectively, more closely related to *L. saxatilis* on the Pacific coast are the periwinkles *Littorina* (*Neritrema*) *subrotundata* (Carpenter, 1864) (synonym: *Littorina newcombiana* Hemphill, 1877) and *Littorina* (*Neritrema*) *sitkana* Philippi, 1846. These latter two species occur from southern Oregon north to Alaska, as well as in the Western Pacific Ocean (Reid, 1996) and occur in a range of morphological-physiological ecotypes, that are closely analogous to those of *Littorina saxatilis* (D. Reid, personal communication, 1997). Should *Littorina saxatilis* reach these northern waters, which are well within their physiological range as noted earlier, competition between *L. saxatilis* and *L. sitkana* and *L. subrotundata* could well occur, given (1) the success in the North Atlantic Ocean of *L. saxatilis,* in terms of habitat breadth, rates of population increase, colonizing ability, and dietary range, and (2) evidence of habitat partitioning among the rock-dwelling *Neritrema* species in the North Atlantic Ocean, offering support for the hypothesis of potential competition (Reid, 1996, and D. Reid, personal communication, 1997).

Parasite loads, particularly trematodes, in these newly established California populations have not yet been analyzed. In this regard, it will be of interest to determine which parasites may have accompanied *L. saxatilis* from the Atlantic Ocean compared to which parasites *L. saxatilis* may gain from Pacific littorines. Of particular interest would be determining long-term shifts in introduced versus native trematode infections.

Finally, if it becomes widespread and common, *Littorina saxatilis* may provide a new shell resource for juvenile hermit crabs (pagurid anomurans) on the Pacific coast. While small native littorines are abundant in San Francisco Bay, it will be of interest to see if hermit crabs exhibit shell selection preferences when offered a choice between native littorines and *Littorina saxatilis.*

OTHER POTENTIAL LITTORINE INVASIONS IN SAN FRANCISCO BAY

We have found two other North Atlantic Ocean periwinkles, *Littorina littorea* and *Littorina obtusata* Linnaeus, 1758, on seaweed imported with baitworms to the San Francisco Bay area (Cohen et al., unpublished observations) and Newport Bay (Carlton, 1992). Living individuals and small groups of *Littorina littorea* were found on occasion in the late 1960s and 1970s on the eastern shore of San Francisco Bay, and a living specimen was found by one of us (ANC) on the western shore of the Bay in 1995, but no established populations are known (Carlton, 1969; Cohen & Carlton, 1995, page 203). No living *Littorina obtusata* have been found in the Bay. However, there appear to be no ecological or physiological limitations that would prevent establishment of these two species on the North American Pacific coast.

ERADICATION?

The eradication of *Littorina saxatilis* from San Francisco Bay might be possible. The two known populations are intertidal, readily accessible, and between them occupy an area of less than 50 square meters. However, it is unclear what government entity would have jurisdictional authority to conduct such an eradication or what regulatory issues would need to be addressed (J. Yamauchi, personal communication, 1996). No tested eradication methods are known to us. Possible methods would include covering the sites with sediment, removing the rocks and sediment (along with the snails), or treating the sites with steam. Continuous harvesting of the population by hand would likely be unsuccessful, as this fecund and often cryptically colored (when fungus infections turn the shell dark and black-spotted) snail hides deeply in inaccessible crevices on large rocks, and tiny individuals are nearly impossible to find among thousands of living and empty barnacles.

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A Qualitative ^{31}P NMR Investigation on the Effects of Exposure to Lead, Cadmium, or Mercury on the Energetic Status of the Pulmonate Gastropod, *Biomphalaria glabrata* (Say)

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Abstract. The present study employed *in vivo* ^{31}P NMR spectroscopy to examine the effects of dissolved lead, cadmium, or mercury chlorides on the levels of phosphorus metabolites in *Biomphalaria glabrata,* a potential bioindicator of heavy metal pollution in fresh water. Snails surviving chronic exposure for 4 or 8 wk to metals at approximately their LC_{50} displayed normal ^{31}P NMR spectra with little effect on the relative levels of NMR observable phosphorus metabolites. Acute exposure to these metals at levels several-fold greater than their LC_{50} for 42 hr prior to analysis also failed to affect the ^{31}P NMR spectrum, indicating that snails surviving heavy metal exposure remain viable and are very tolerant to metal poisoning. Acute exposure of previously unexposed snails to mercury at 5, 10, and 15 μM resulted in significant and progressive changes in the relative levels of phosphorus metabolites in the NMR spectrum. After 6 hr of exposure to 15 μM mercury, the relative levels of ATP and the energy index [(ATP)(phosphoarginine)/Pi] approached 50% of their initial values.

INTRODUCTION

Inorganic and organic aquatic pollution commonly accompany industrialization of developing countries (Denny, 1987). In Egypt, heavy metal contamination of the River Nile by industrial activities in areas surrounding the city of Cairo has become a serious concern to government authorities (Lasheen, 1987). The development of methods for monitoring pollutant levels is an important priority (Olade, 1987; Petrele, 1991).

Mollusks are known to accumulate heavy metals to concentrations several-fold greater than those of the surrounding aquatic environment (Phillips & Rainbow, 1993), and thus these organisms may serve as valuable bioindicators of heavy metal pollution (Rainbow & Phillips, 1993). *Mytilus edulis* Linnaeus, 1758, for example, is now employed for indicating heavy metal contamination in marine environments (Cossa, 1989). Recently, we reported the accumulation of lead, cadmium, and mercury in the tissues of the pulmonate gastropod *Biomphalaria glabrata* (Say, 1818), a vector of the human disease schistosomiasis, and suggested the use of this species and others of the genera as potential bioindicators in appropriate freshwater environments (Abd Allah et al., in press).

Although extensive studies have been conducted on the uptake, accumulation, and detoxification of heavy metals in various molluscan species (George & Viarengo, 1985), little is known of the overall effects of heavy metals on energy metabolism or of how sublethal levels of toxicants affect the levels of high energy phosphorus metabolites. *In vivo* ^{31}P NMR spectroscopy has been successfully employed to examine the effects of physical and chemical damage on phosphorus metabolism in a variety of tissues and organisms (Gadian et al., 1979; Gadian, 1982). The present study was conducted to investigate the effects of acute and chronic exposure to heavy metals on the relative levels of phosphorus metabolites in *B. glabrata* and to assess the potential for using ^{31}P NMR spectroscopy as an indicator of the energetic status of this freshwater snail species.

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MATERIALS AND METHODS

Snail Maintenance

Stock colonies of albino M-line *B. glabrata* (Newton, 1955) were reared in commercial spring water (Arrowhead®, Monterey Park, California) in 7.5 L glass aquaria maintained at 25 ± 1°C under a 12 hr light/dark photocycle. Snails were fed on fresh romaine lettuce supplemented with Aquarian® fish food (Mardell Laboratories, Waltham, United Kingdom). During experiments, populations of 50 reproductively active adult snails (11–13 mm) were maintained in approximately 2.5 L of spring water (Arrowhead) and were housed in a Percival environmental chamber at 28 ± 1°C.

Exposure of Snails to Lead, Cadmium, or Mercury

Snails were chronically exposed for 4 or 8 wk to 100 μM lead (2^+), 0.25 μM cadmium, or 1 μM mercury (2^+) chloride salts dissolved in spring water. Metal solutions were replaced weekly. Under these conditions the above concentrations were previously demonstrated to cause approximately 50% mortality at 8 wk exposure (Abd Allah et al., in press). After 4 or 8 wk, 12 snails from each test concentration and a similar group of unexposed snails maintained in spring water only were gently crushed between two petri plates to shatter the shell. The broken shells were rinsed away from the snail viscera with spring water and any adhering shell fragments were carefully removed with forceps. After shell removal, snails were perfused for 2 hr in fresh spring water, and *in vivo* ^{31}P NMR analyses were conducted, all as described below. Additional experiments were conducted to examine the effects of acute exposure to higher levels of heavy metals. In the first experiment, snails were exposed for 42 hr to lead, cadmium, or mercury chloride at 600 μM, 2.5 μM, and 6 μM, respectively, dissolved in spring water. Twelve snails with their shells removed as described above were perfused for 2 hr in the spring water containing the heavy metals at the above concentrations. Last, previously unexposed snails with shells removed were perfused with spring water containing 10, 15, or 20 μM mercury chloride. Prior experiments demonstrated that snails exposed to heavy metals at these concentrations died within a few days.

Perfusion of *B. glabrata* in the NMR Spectrometer

Following shell removal, snails were placed in the bottom of a 12 mm glass NMR tube, on top of a 1 cm glass spacer and secured above with a small wad of glass wool. A short length of teflon tubing attached to a 2 m, 1.5 mm diameter piece of polypropylene tubing was inserted through a silicone stopper, into the snail mass. The tubing was then connected through a perfusion pump to a bubble trap and a fluid reservoir containing the perfusate. The latter was gassed with air through tubing attached to a small air pump. The perfusate was thus continuously pumped through the tissue bed and exited the NMR tube through a second length of polypropylene tubing into a waste container. The snails were perfused at a rate of approximately 1.5 to 2 ml/min. The apparatus employed was illustrated by Thompson & Lee (1985).

^{31}P NMR Analyses

^{31}P NMR spectra were generated at 121.5 MHz in a wide-bore Nicolet 300 spectrometer. The instrument was interfaced with a Nicolet 1280 computer and operated in the pulsed Fourier transform mode. A radiofrequency pulse of 45° (25 μsec), 409.5 msec acquisition time and 1 sec delay were the parameters employed to ensure maximum signal to noise ratio under non-saturating conditions. *In vivo* spectra were generated from 4800 data acquisitions. Before perfusion, a deuterium oxide field-frequency lock was used. Analyses were conducted at approximately 22°C.

^{31}P NMR resonances in *in vivo* spectra were assigned based on chemical shift and a variety of analytical and NMR methods previously described (Thompson & Lee, 1987). For assessing and comparing the compositions of the *in vivo* ^{31}P NMR spectra between the various trials, computer simulations based on Lorenzian line shapes were conducted to eliminate the contributions of overlapping spectral components. A typical fitted spectrum for control unexposed snails is shown in Figure 1 together with the original spectrum and residual determined by computer subtraction of the original spectra from the fitted spectra. Although the signals of biological NMR spectra seldom display exactly Lorenzian line shape, the total integrated intensities of the computer simulations for all samples were $> 99\%$ of the actual integrated intensities of each individual *in vivo* spectrum. Fitted and resolved spectra are shown in Figures 1 and 2. In a few cases, resolution of the simulated spectra was not possible—for example, peak 11 and the minor downfield peak in some of the spectra of Figure 2. The levels of ATP, phosphoarginine (AP), and inorganic phosphate (Pi) were monitored hourly for 6 hr during acute exposure to mercury, and an energy ratio, [(ATP)(PA)]/Pi, was calculated as an indicator of the overall energy status of the snail preparation. Time course data were presented as the percentage change from the initial value. During these experiments spectra were generated from 2400 data acquisitions.

RESULTS

In vivo ^{31}P NMR Spectrum

The *in vivo* ^{31}P NMR spectrum of perfused *B. glabrata* is shown in Figure 1. Numerous phosphorus metabolites were observed and the resonance for the phosphorus of ATP was clearly resolved (Figure 1). Spectral assignments are as follows: (1) β ATP; (2) glucose phosphate of uridine diphosphoglucose (UDPG); (3) nicotinamide adenine dinucleotide and uridine phosphate of UDPG; (4) α-ADP + α-ATP; (5) β ADP + γ ATP; (6) phosphoarginine; (7) free phosphatides, principally phosphatidylcholine; (8) glycerophosphorylcholine and diphosphatidylglycerol; (9) inorganic phosphate; (10) phosphomonoesters, principally sugar phosphates; and (11) ceramideaminoethylphosphonate.

Effects of Chronic Exposure to Heavy Metals

The ^{31}P NMR spectrum was not affected in any consistent or significant way after 4 or 8 wk exposure to lead,

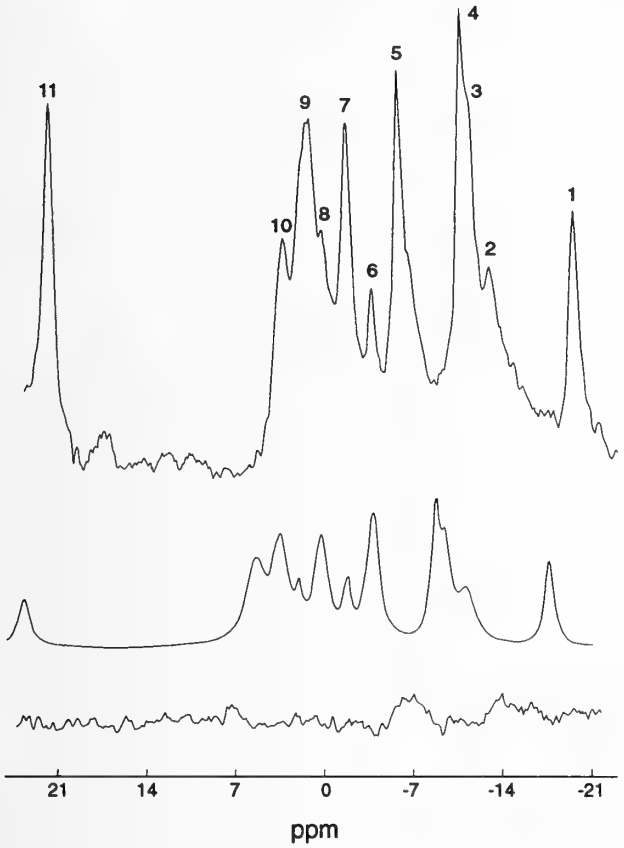

Figure 1

In vivo ^{31}P NMR spectrum of *Biomphalaria glabrata.* Snail shells were removed as described in the text. Chemical shifts are shown relative to orthophosphoric acid in the usual manner. Spectrum is shown with 30 Hz line broadening and was generated from 12 individual snails with a combined fresh weight of approximately 1.5 g. Spectral assignment of the major phosphorus components is outlined in Results. Relevant assignments used for calculating the phosphorus index are: (1) β ATP, (6) phosphoarginine and (9) inorganic phosphate. Shown below is the computer simulated spectrum for the control snails and the residual difference between the observed and the simulated spectra.

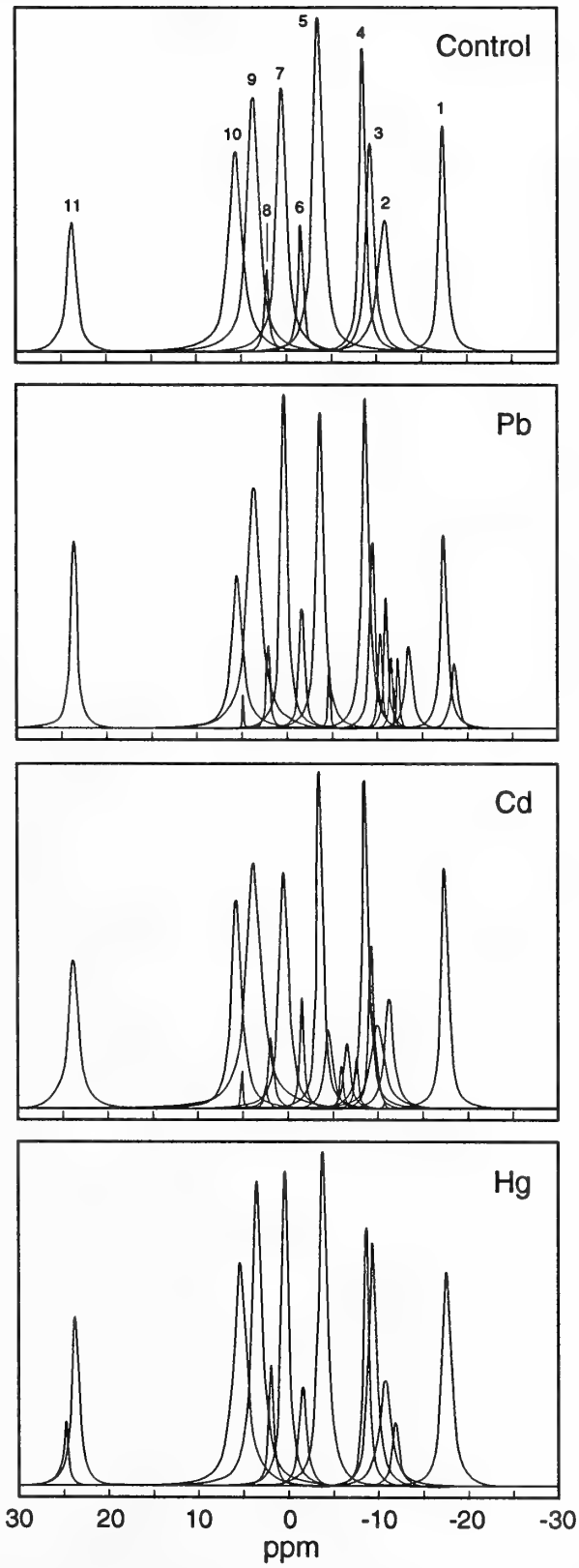

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Figure 2

In vivo ^{31}P NMR spectra of whole-shelled *Biomphalaria glabrata* unexposed and exposed to heavy metals for 4 wk. (a) Unexposed control snails, (b) snails exposed to 100 μM lead, (c) 0.25 μM cadmium, and (d) 1 μM mercury chloride. Spectra are shown with 30 Hz line broadening and were generated from 12 individual snails with a combined fresh weight of approximately 1.5 g. Individual spectra are shown relative to the most intense phosphorus resonance of each spectrum. All spectra were computer simulated from the originals as shown in Figure 1, and the simulated spectra were resolved to show individual spectral components. The minor peaks are unassigned.

cadmium, or mercury chloride at 100, 0.25, or 1 μM, respectively. Spectra for 4 wk exposure are shown in Figure 2. Computer simulations allowed direct comparison of peak heights and areas between control and exposed snails and demonstrated that exposed snails had similar relative ATP levels as those observed in controls. Spectra are shown relative to ceramide aminoethylphosphonate (peak 11) which served as an internal standard. Ceramide aminoethylphosphonate is observed principally in the snail's albumin gland (Thompson & Lee, 1985). The results shown are consistent with those of preliminary analyses of snails similarly exposed to these heavy metals for periods of several weeks. Differences in the relative levels of the major spectral components between unexposed and exposed snails and between groups of exposed snails were generally within the normal variation observed between snails (± 10%) as established by traditional biochemical analyses (Thompson & Yamada, 1984), and subsequently verified by ^{31}P NMR spectroscopy (Thompson & Lee, 1987). Resolution of the simulated spectra suggests the presence of additional, but minor components within the major peaks of the *in vivo* ^{31}P NMR spectrum. Identification of these lesser phosphorus metabolites will require more extensive chemical analyses of tissue extracts than those conducted thus far, and the majority of these components remain unassigned at this time.

Effects of Acute Exposure to Heavy Metals

Exposure to 600 μM lead, 2.5 μM cadmium, or 6 μM mercury for 42 hrs followed by perfusion for 2 hr in these metal solutions also failed to demonstrate any significant effects on the ^{31}P NMR of *B. glabrata* (spectra not shown). Acute exposure of previously unexposed snails to higher levels of mercury chloride, however, did result in observable spectral changes. At 10 and 15 μM mercury, significant decreases in signal intensities for phosphoarginine and ATP were evident. Accompanying these effects was an increase in the relative intensity of inorganic phosphate. As reflected by the relative level of ATP and the energy index, the above changes were generally progressive over the exposure period (Figure 3). The relative level of ATP in snails exposed to 15 μM mercury chloride approached 50% of its initial level only after 6 hr exposure.

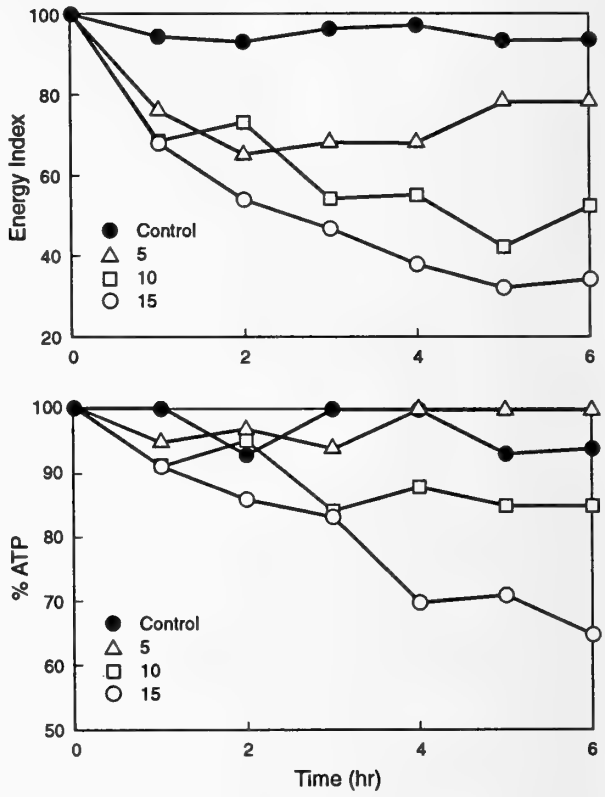

Figure 3

Typical effects of acute exposure to mercury chloride on the relative level of ATP and the energy index [(ATP)(PA)]/Pi of *Biomphalaria glabrata* determined by monitoring the *in vivo* ^{31}P NMR spectrum. Data were generated from 12 individual snails with a combined fresh weight of approximately 1.5 g. In the case of snails exposed to mercury, the first spectrum was generated prior to mercury exposure. β ATP and the energy index are both shown as a percentage of their initial value.

DISCUSSION

The qualitative composition of the *in vivo* ^{31}P NMR spectrum of *B. glabrata* was similar to that previously reported for this species (Thompson & Lee, 1985, 1987). The contribution of phosphoarginine to total phosphorus was relatively low, and the level of inorganic phosphorus relative to ATP, relatively high. This, however, was not due to handling, shell removal, or other apparent stress. Earlier analyses conducted on intact snails have confirmed that the relative levels of phosphorus metabolites in snails without shells reflect those of intact snails (Thompson & Lee, 1985; Thompson et al., 1991). The relatively low level of phosphoarginine in *B. glabrata* is consistent with the ciliary locomotion typical of this snail, as described by Thompson et al. (1993).

The energy status of *B. glabrata* surviving exposure to toxic LC_{50} levels of lead, cadmium, or mercury appeared to be minimally affected. ^{31}P NMR spectroscopy, therefore, will likely prove of limited value for monitoring the impact of sublethal levels of these heavy metals. The present results are nevertheless important because they confirm that *B. glabrata,* and perhaps other closely related snail species, can serve as useful bioindicators of heavy metal pollution in freshwater environments. Snails remained viable at metal concentrations where snails accumulate significant amounts of metals in their tissues. Indeed, previous studies demonstrated that snails exposed

to lead, cadmium, or mercury at much lower concentrations than the LC_{50} levels tested in this investigation accumulate readily detectable levels of these metals (Abd Allah et al., in press).

To examine the potential toxic effects of extremely high levels of heavy metals on the ^{31}P NMR spectrum of *B. glabrata,* snails were acutely exposed to mercury at 5, 10, and 15 μM. As the mercury level was increased, the relative levels of ATP and phosphoarginine declined while inorganic phosphate increased, all effects expected to arise from loss of respiratory capability and death. At all mercury concentrations the relative levels of ATP declined less than the energy index, clearly indicating the role of phosphoarginine as an "energy buffer" against ATP loss, as previously demonstrated in *B. glabrata* by Thompson et al. (1993). The mercury concentrations tested, however, are much higher than those encountered in the environment, and the results, therefore, represent an extreme situation with little relevance to the natural environment. Again, these results serve to illustrate the relative tolerance of this species to metal poisoning.

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THE VELIGER

Description of a New Species in the Genus *Tambja* Burn, 1962 (Gastropoda: Nudibranchia: Polyceratidae) from Southern Spain

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Abstract. A new species of *Tambja* is described from the western Mediterranean on the coast of southern Spain. The external and internal features of this species are compared with those of the known Atlantic species of the genus. *Tambja* ***marbellensis*** sp. nov. varies in color between dark blue, almost black, and dark greenish blue. It has a yellow band on the edge of the notum and the foot, and other bands of the same color and differing in length, on the notum, flanks, and tail. The radula is typical of the genus *Tambja,* with the inner lateral tooth having a conspicuous denticle on the inner edge of the primary cusp. The second inner lateral tooth also has a small cusp. The reproductive system has a differentiated prostate from the deferent duct, and the bursa copulatrix and the seminal receptacle are similar in size.

INTRODUCTION

To date, the only known species of the genus *Tambja* Burn, 1962, in European waters is *T. ceutae.* Described some years ago by García-Gómez & Ortea (1988), it was collected on the coast of Ceuta (African side of the Strait of Gibraltar). This species has been recorded recently on the coast of the Azores Archipelago (Wirtz & Martins, 1993; Wirtz, 1995) and the Canary Islands (Ortea et al., 1996).

Frequent samplings along the coast of the Province of Malaga (southern Spain, western Mediterranean) have permitted us to find specimens of a second undescribed species of *Tambja,* which is described in this paper.

SYSTEMATIC DESCRIPTION

Suborder DORIDACEA
Family POLYCERATIDAE Alder & Hancock, 1845
Genus *Tambja* Burn, 1962
Tambja ***marbellensis*** Schick & Cervera, sp. nov. (Figures 1–3)

Material: Holotype: One specimen, 45 mm in length, collected at 10 m depth, Torre del Cable (Marbella, Málaga) (36°52′35″N, 04°30′01″W), southern Spain, July 1995, K.L. Schick coll. This specimen has been deposited in the Museo Nacional de Ciencias Naturales of Madrid, with the catalogue number 15.05/26031.

Paratype: One specimen, 12 mm in length, collected at 10 m depth Torre del Cable, May 1995, K.L. Schick coll. A photograph of this specimen and its radula have been deposited in the Museo Nacional de Ciencias Naturales, with the catalogue number 15.05/27819. We have deposited only the photograph and radula, because the specimen died early in the aquarium before we were able to preserve it. The specimen was slightly decomposed and all of the internal structures, with the exception of the radula, could not be studied.

Diagnosis: Body limaciform with widened head; notum with smooth edge and tail. Ground color dark blue or dark greenish blue. Edge of notum and foot yellow; notum flanks of body and tail with several yellow stripes different in length. Outer surface of gill rachis yellow and rhinophoral sheaths bordered with yellow. Yellow stripes and marks shaded with brown. Rachidian tooth wider than tall and notched at anterior edge; inner lateral radular

→

Figure 1

Tambja ***marbellensis*** Schick & Cervera, sp. nov. Dorsal view (A), lateral view (B), and detail of the anterior part (C) of the holotype. D. Detail of the rhinophore. E. Dorsolateral view of the paratype. Key: br, brownish; db, dark blue; dgb, dark greenish blue; ye, yellow.

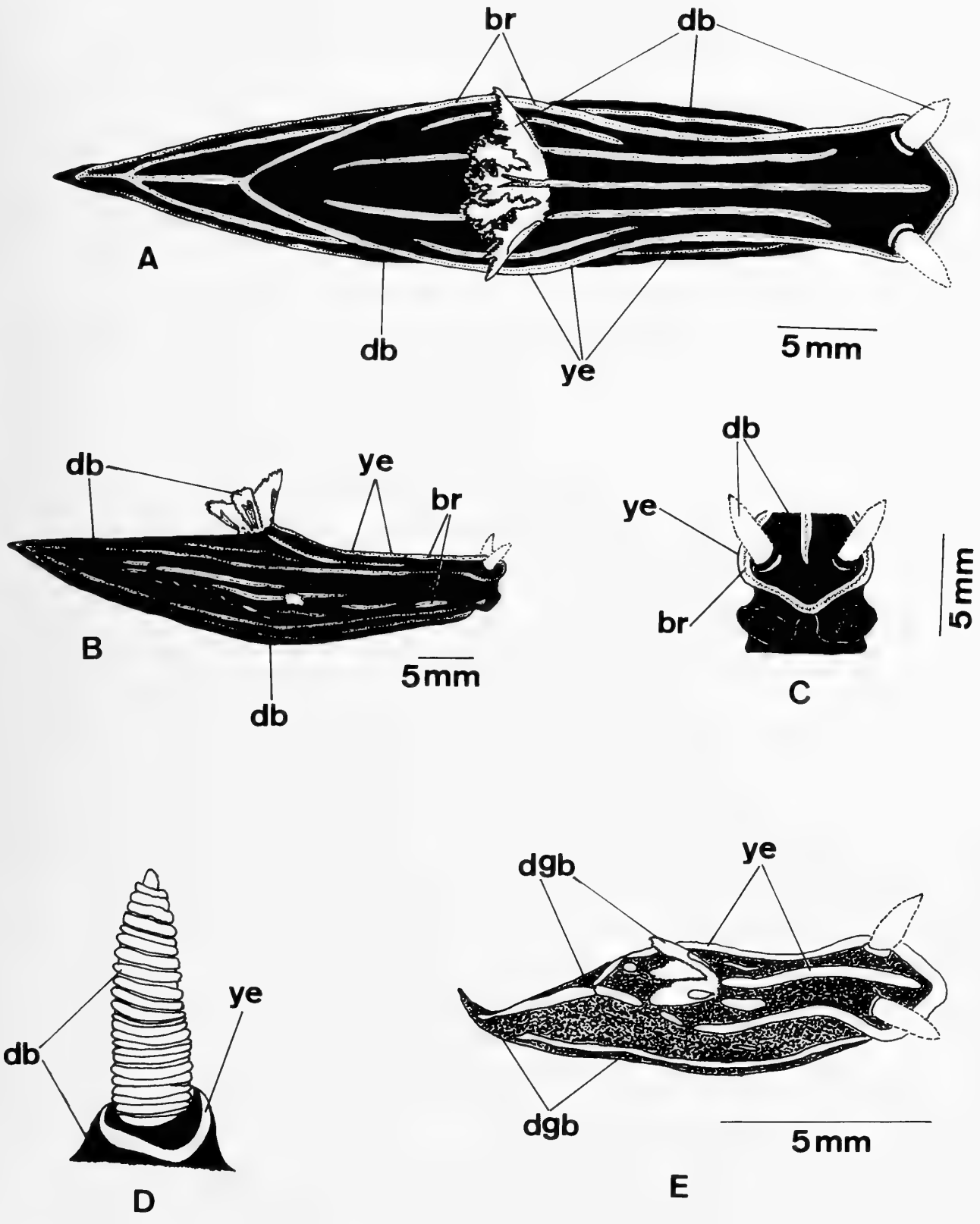
br
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Table 1

Comparison of the Atlantic species of the genus *Tambja* Burn, 1962.

	T. gratiosa (Bergh, 1890)	*T. capensis* (Bergh, 1907)	*T. divae* (Marcus, 1958)	*T. oliva* Meyer, 1977	*T. fantasmalis* Ortea & García-Gómez, 1986	*T. ceutae* García-Gómez & Ortea, 1988	*T. anayana* Ortea, 1989	***T. marbellensis***
Ground color	Light yellowish with random round grey-green spots on the back and sides. Blue-black also occurs on forehead, edge of foot, and rim of oral tentacles.	Deep blackish blue or black. The sole of the foot somewhat yellowish white. Edge of notum green.	Scarlet with white dots	Deep olive green to light green or olive yellow. Microscopic flecks of yellow, blue or turquoise. Tips of tail and oral tentacles light to dark purple or blue-green. Two large light grey spots behind rhinophores.	Violet-blue-black, 2 phosphorescent green bands on the back, 2 on each flank.	Greenish blue or dark blue, 5 yellow lines on the notum and another 2 on each flank. All lines bordered with dark blue-black. Two large dark grey spots behind the rhinophores.	Light khaki green, some black points. Edge of the notum and back of the tail violet. Violet lines between the rhinophores and behind the gills.	Dark blue or dark greenish blue. Several yellow lines on the notum and the flanks. Edge of the notum and foot yellow. Adults have the yellow lines shaded by brown.
Rhinophores	Yellowish with blue black clubs	Blue-black	Scarlet	Purple or white with opaque cream spots	Dark blue (including their sheaths)	Dark blue; dark blue sheaths, the margin bordered with yellow.	Light green, except the lower ⅔ of the anterior side that is violet.	Dark blue; dark blue rhinophoral sheaths, but the margin bordered with yellow.
Gills	Bi-tripinnate. Blue-black.	7, tripinnate. Same color as the body.	3, tripinnate. White.	4–5, pinnate. Same color of the body, but the tips are light to dark purple or blue-green.	5, tripinnate. Dark blue outer side with 2 green lines on their lower half; green inner side on their lower half and blue on the upper half.	5, tripinnate. Yellow outer and inner side of the rachis, except a dark blue wedge on the outer side. All the leaves dark blue.	3, tripinnate. Light green.	5, tripinnate. Dark blue with a yellow outer surface of the rachis. Yellow marks of the adults shaded by brownish.
Edge of the notum	Smooth	Smooth	Smooth	Smooth	Smooth	With blue or greenish blue conical papillae	Smooth	Smooth
Tail	Smooth	Smooth	Smooth	Smooth	Smooth	With blue or greenish blue conical papillae	Smooth	Smooth

Table 1

Continued.

	T. gratiosa (Bergh, 1890)	*T. capensis* (Bergh, 1907)	*T. divae* (Marcus, 1958)	*T. oliva* Meyer, 1977	*T. fantasmalis* Ortea & García-Gómez, 1986	*T. ceutae* García-Gómez & Ortea, 1988	*T. anayana* Ortea, 1989	*T. **marbellensis***
Radula	16 × 1–3.0–1.R.0–1.1–3. Inner lateral tooth bicuspid (both cusps equally strong).	14–19 × 5–6.1.R.1.5–6. Inner lateral tooth monocuspid.	16 × 5–6.1.R.1.5–6. Inner lateral tooth monocuspid.	12–13×4.1.R.1.4. Inner lateral tooth bicuspid.	13 × 4.1.R.1.4. Inner lateral tooth monocuspid.	15 × 4.1.R.1.4. Inner lateral tooth monocuspid.	28 × 3–4.1.R.1.3–4. Inner lateral tooth bicuspid in rows 1st to 22th (with progressive decreasing of the 2nd cusp), monocuspid in rows 23 to 28.	13–16 × 3–4.1.R.1.3–4. Inner lateral tooth bicuspid.
Reproductive system	Bursa copulatrix bigger than the seminal receptacle. The oviduct has a small accessory gland. No vestibular gland is reported. Penis with spines.	Deferent duct lacking a prostate morphologically differentiated. Bursa copulatrix bigger than the seminal receptacle. A vestibular gland present[a]. Penis with spines.	Deferent duct with a prostate slightly morphologically differentiated. Bursa copulatrix bigger than the seminal receptacle. No vestibular gland is reported. Penis with spines.	Deferent duct with a prostate slightly morphologically differentiated. Gland of indeterminate function connected to bursa copulatrix by a short duct. Penis with spines[b].	Prostate morphologically not differentiated. Bursa copulatrix bigger than the seminal receptacle. Vestibular and penial glands present. Penis with spines.	Prostate morphologically differentiated. Bursa copulatrix bigger than the seminal receptacle. Vestibular gland present. Penis with spines.	Not described	Prostate morphologically differentiated. Bursa copulatrix and seminal receptacle similar in size. Vestibular gland present. Penis with spines.
Geographical range	West of Florida keys (Gulf of Mexico)	Cape Province (South Africa)	Arraial do Cabo, Cabo Frio (Brazil).	Caribbean coast of the Panama canal zone; Bahamas.	Cape Verde	Azores, Canary Islands, strait of Gibraltar, western Mediterranean	Cape Verde	Western Mediterranean
References	Bergh (1890)	Bergh (1907); Macnae (1958); Gosliner (1987)	Marcus (1958)	Meyer (1977); Redfern & Worsfold (pers. com.)	Ortea & García-Gómez (1986)	García-Gómez & Ortea (1988); Wirtz & Martins (1993); Wirtz (1995); present study	Ortea (1989)	Present study

[a] Macnae (1958) does not refer to the existence of this gland.

[b] Meyer (1977) does not draw the arrangement of the reproductive system.

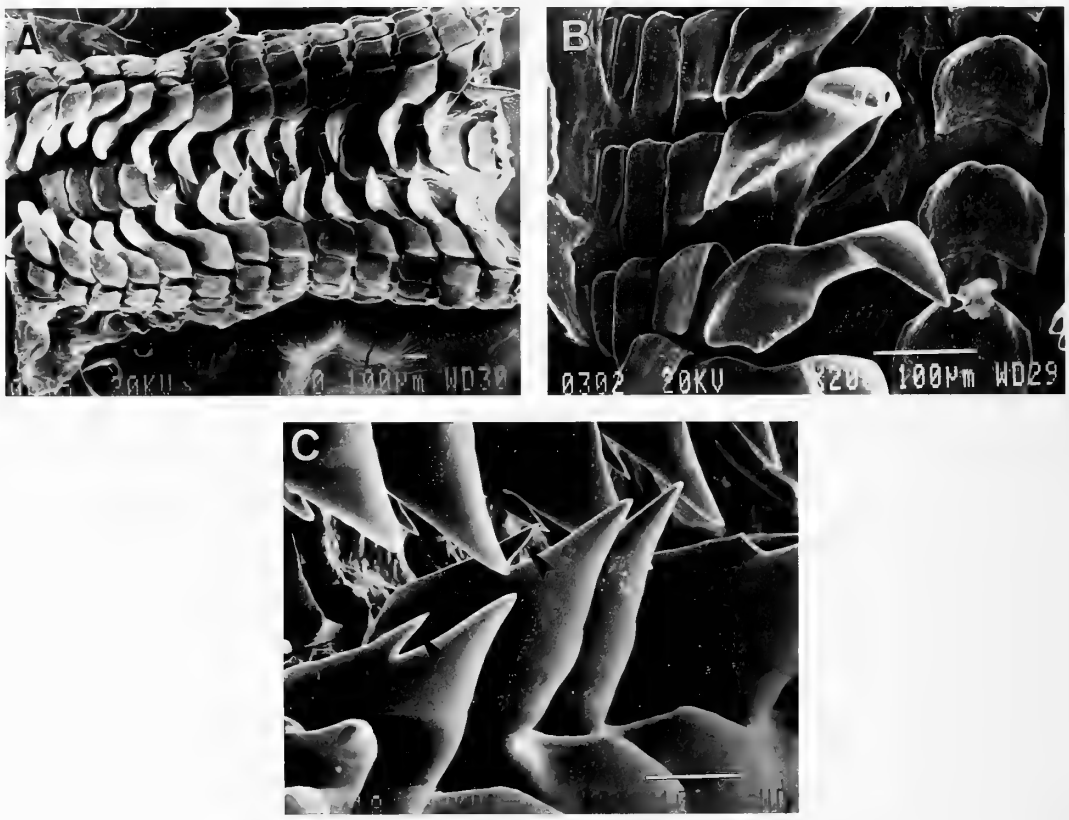

Figure 2

*T. **marbellensis*** Schick & Cervera, sp. nov. A. General view of the radula of the holotype. B. Detail of the rachidian and lateral radular teeth of the paratype. C. Detail of the dorsal view of the cusps of the inner lateral radular teeth of the holotype (arrow heads indicate the inner denticle).

tooth hooked, with large bicuspid primary cusp; second inner lateral tooth with small cusp. Rounded bursa copulatrix and pyriform seminal receptacle similar in size; prostate well differentiated and vestibular gland well developed.

Description: Body limaciform with widened head; notum, and its edge and tail smooth. Oral tentacles short and dorsoventrally flattened. Dark blue rhinophores have 25 lamellae and conical clavus (Figure 1D). Smooth sheaths dark blue bordered with yellow. Five gills tripinnate and non-retractile, situated around anal papillae.

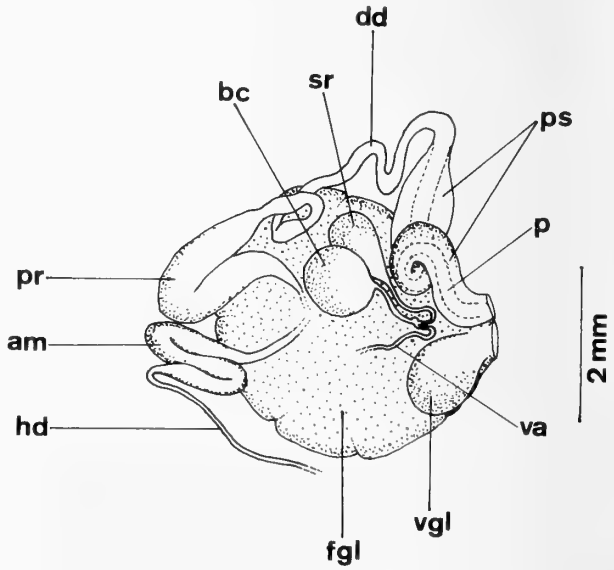

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Figure 3

*T. **marbellensis*** Schick & Cervera, sp. nov. Reproductive system. Key: am, ampulla; bc, bursa copulatrix; dd, deferent duct; fgl, female gland; hd, hermaphroditic duct; p, penis; pr, prostate; ps, penial sheath; sr, seminal receptacle; va, vagina; vgl, vestibular gland.

Three anterior gills more highly developed. Gills dark blue with yellow outer surface of rachis. Ground color varies between dark blue, almost black, and dark greenish blue. Yellow band around edge of notum. Notum with several stripes of this color (Figure 1). Mid line extending from anterior part of head, near edge of notum, to middle gill, branching onto outer side of rachis. Another two lines start from posterior cephalic region and run between middle line and edge of notum reaching gills, extending on outer side of each rachis (Figure 1A, C). Two other yellow lines start from notal region in front of gills and run very close to edge of notum ending in postbrachial region. Another two yellow lines start from base of gills to posterior region of notum, but without reaching edge. Edge of foot also bordered by yellow band, which joins that of edge of notum via band of same color that runs dorsally down tail. Several yellow lines, varying in number and length according to size of specimen, distributed on both flanks of body (Figure 1B). In adult specimen, only one of these lines runs from cephalic region as far as dorsal line on tail. Central region of almost all these lines was brownish shade, in 45 mm specimen (Figure 1A).

With respect to internal anatomy, radular formula of 12 mm specimen 13 × 3–4.1.R.1.3–4 and that of 45 mm specimen 16 × 3–4.1.R.1.3–4 (Figure 2A). Rachidian tooth, wider than tall, notched at anterior edge. Inner lateral tooth hooked with large primary cusp, with conspicuous denticle on inner edge (Figure 2A, B), and smaller triangular basal cusp (Figure 2C). Remaining lateral teeth scalelike and less developed than former (Figure 2B), although second inner lateral has small cusp. Reproductive system (Figure 3) with hermaphroditic duct that continues, as S-shaped ampulla. Bursa copulatrix rounded; seminal receptacle pyriform, both similar in size. Vagina very straight, entering female gland almost at central region. Oval vestibular gland well developed. Deferent duct with well-differentiated prostate. Penis armed with numerous hooked spines.

DISCUSSION

To date, only seven species of the genus *Tambja* have been described from Atlantic waters. The most important features of these species are compared in Table I. The external and internal features of *T. **marbellensis*** permit it to be distinguished from the remaining cogeneric Atlantic species, including *T. ceutae,* which is the most similar species. *T. **marbellensis*** lacks the conical papillae of the notal ridge and tail characteristic of *T. ceutae,* which are even more conspicuous in young specimens (personal observation), the yellow lines on the inner surface of the rachis of the gills of the second species, and also the two large dark grey spots behind the rhinophores of that species, but it has the yellow lines shaded by brown that do not occur in those of *T. ceutae.* With respect to the internal anatomy of both species, the inner lateral tooth is bicuspid in *T. **marbellensis*** and monocuspid in *T. ceutae,* and the two allosperm receptacles are similar in size in the former species and different in the latter. Moreover, the deferent duct in *T. ceutae* is more elongate and coiled than in our species.

As García-Gómez & Ortea (1988) pointed out previously, the species attributed to *T. diaphana* (Bergh, 1878) (quoted as *Nembrotha*) by Pruvot-Fol (1927) from the Moroccan coast could constitute a new species of this genus, although the exact identity of that species would require the study of additional specimens from the same locality or nearby areas. On the other hand, we agree with the opinion of Drs. Richard Willan and Clay Carlson (personal communication) that since every species of the genus *Tambja* has a limited geographical range, it is practically impossible that the Pruvot-Fol species is conspecific with Bergh's *T. diaphana* from the Palau Islands (tropical Pacific). Our species can be distinguished from the Pruvot-Fol species since, according to her description, it has a sulphur yellow ground color with emerald green lines on the back that join between them before the rhinophores and behind the gills.

Etymology: The specific name refers to Marbella, the type locality of the species.

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THE VELIGER

Digestive Tract and Functional Anatomy of the Stomach of *Nausitora fusticula* (Jeffreys, 1860) (Bivalvia: Teredinidae)

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Abstract. The configuration of the digestive tract and a detailed description of the anatomy and main ciliary currents of the stomach of *Nausitora fusticula* are given and compared with other known teredinids. The stomach is of the elongate type and differs strikingly from all other known elongate stomachs in the Teredinidae by the possession of two right caeca, both invaded by the major typhlosole. This fold is also peculiarly accompanied all along its course inside the stomach by the minor typhlosole and the sorting area **SA7**. These three structures enter the left caecum and the anterior and posterior right caeca as well, within which they segregate the openings of the normal from those of the specialized digestive diverticula, showing that those three pockets are the main sites where final separation of wood from suspended filtered particles occurs. The presence of seven well-defined sorting areas on the stomach walls reveals a low selectivity exercised by the organs and structures in the pallial cavity, and specialization of the stomach to deal with a great variety of isolated particles. The moderate size of the appendix and mid-gut, the weakly developed typhlosole of the appendix, and absence of fecal pellets in the species are indicative of a predominantly suspension-feeding habit.

INTRODUCTION

The first comprehensive study of the digestive tract of the teredinids, which gave an excellent illustrated account of the internal anatomy of the stomach was that of Lazier (1924), concerning *Teredo navalis* Linnaeus, 1758. In that work Lazier reviewed previous literature on the digestive tract in the family, the main ones being those of Quatrefages (1849) and Beuk (1899), which gave only brief anatomical accounts of *Teredo fatalis* Quatrefages, 1849 [which is *Nototeredo norvagica* (Spengler, 1792) according to Turner (1966; 1971)], and *Teredo* spp., respectively, and the work of Sigerfoos (1908), which described and illustrated the development of the alimentary canal of *Xylotrya gouldi* Bartsch, 1908 [which is *Bankia gouldi* (Bartsch, 1908) according to Turner (1966, 1971)], from the larval stage to the adult. Besides Lazier (1924), Potts (1923) described the digestive tract of *Teredo* sp, with emphasis on the structure and function of the digestive diverticula.

Despite the considerable amount of literature on Teredinidae which has appeared after Lazier (1924), only the following deal with the anatomy of the digestive tract: Purchon (1960) analyzed the internal anatomy of the stomach of *Psiloteredo amboinensis* Take & Habe, 1945 [which is *Spathoteredo obtusa* (Sivickis, 1928) according to Turner (1966; 1971)], *Teredo manni* Wright, 1866 [no reference in Turner (1966, 1971), but Turner (1966) indicates *Kuphus* ? *mannii* Wright, 1866, as *Dicyathifer manni* (Wright, 1866)] and *T. navalis,* and gave a very detailed illustrated account of the functional anatomy of the stomach for *P. amboinensis* only; Bade et al. (1964) described the digestive system of *Bankia (Bankiella) minima* Blv., Nach, Roch [no reference in Turner (1966, 1971), but this author makes reference to *Teredo minima* Blainville, 1828 as *Bankia carinata* (Gray, 1827)]; Turner (1966) described the external anatomy of the stomach of several species of Teredinidae and recognized three distinct types of stomach based on the external topography of this organ in representatives of the subfamilies of Teredinidae; Morton (1970) and Martinez (1987) added new data on the internal structure and functioning of the stomach of *T. navalis*; Morton (1970) made occasional references to the stomach of *Lyrodus pedicellatus* (Quatrefages, 1849); Rancurel (1971) described the microscopic anatomy of the stomach of *Teredo petiti* Recluz [which is *Psiloteredo senegalensis* (Blainville, 1828) according to Turner (1971)] and *Teredo adami* Moll [which is *Neoteredo reynei* (Bartsch, 1920) according to Turner (1971)]; Saraswathy & Nair (1971) described the anatomy of the stomach of *Teredora princesae* (Sivickis, 1928), *Teredo furcifera* von Martens, 1894, and *Nausitora hedleyi* Schepman, 1919; Bazylinski & Rosenberg (1983) described the occurrence of a brush border in the appendix of several *Teredo* and *Bankia* species.

The terminology adopted to describe the stomach in the above-mentioned works differs among authors. This fact, along with the scarcity of detailed illustrations like those of Lazier (1924), Purchon (1960), and Morton (1970), makes comparisons of structures among different species difficult.

The study of the gross anatomy of the digestive tract

and a detailed description and illustrations of the internal structures and functioning of the stomach of *Nausitora fusticula* (Jeffreys, 1860) is the scope of the present paper. It complements a study performed by Lopes & Narchi (1998) on the functional anatomy of the organs and structures in the pallial cavity of this species. Comparisons are made with some of the more important aspects in the descriptions of the above-mentioned authors, and the correlation among structures of the stomach described under different names will also be summarized in order to facilitate future studies on this organ and phylogenetic approaches to the family.

MATERIALS AND METHODS

Logs containing *Nausitora fusticula* were obtained from a mangrove area in the vicinity of the Praia Dura, Ubatuba, São Paulo State, Brazil (22°30′S, 45°15′W), and transferred to and kept in aquarium with salinity 20, in the Laboratory of Malacology at the Department of Zoology, Bioscience Institute, University of São Paulo. Around 100 live, relaxed, and preserved specimens (2–200 mm in length), were analyzed. Most illustrations are composites of several dissections. Only Figures 1, 2, 3, 8B, and 9B were done using a camera lucida.

Magnesium sulfate was used as a relaxing agent. For histological sections, specimens were fixed in Bouin's solution for 24 hours, dehydrated in alcohol, and embedded in paraffin. Sections (6–10 μm thick) were stained with Mallory's triple stain as specified by Pantin (1948).

Ciliary currents were studied using carmine, Acquadag, Carborundum grade F3, and the finest sawdust fragments obtained by rubbing a mangrove log with a dentist's drill.

A lot of 20 complete specimens (valves, pallets, and soft parts) were deposited at the Museu de Zoologia, Universidade de São Paulo (MZUSP) under the registration number 28598.

RESULTS

External Anatomy of the Digestive Tract

The configuration of the digestive tract of *Nausitora fusticula,* and details of particular regions of the same are shown in Figures 1 to 4. The terminology adopted is from Purchon (1956, 1957, 1958, 1960) for the anatomy of the stomach and from Morton (1970, 1978) for the digestive diverticula.

The slitlike mouth (**mo**) lies dorsal and slightly posterior to the foot and opens into a short, dorso-ventrally flattened esophagus (**o**). The latter follows a course slightly skewed to the left before opening into the antero-dorsal wall of the stomach through an aperture smaller than the mouth.

The stomach is an elongate organ with an anterior, globular region (**ar**), sheltered within the limits of the shell valves; a median, lengthened region (**mr**), almost uniformly cylindrical; and a posterior region, consisting of two parallel and cylindrical structures forking from the posterior end of the median region. These two latter regions of the stomach remain outside and posterior to the limits of the shell valves.

The anterior globular region of the stomach gives rise to the dorsal hood (**dh**), left caecum (**lc**), left pouch (**lp**), style-sac (**ss**) (Figure 2), and to the anterior right caecum (**arc**) (Figure 3).

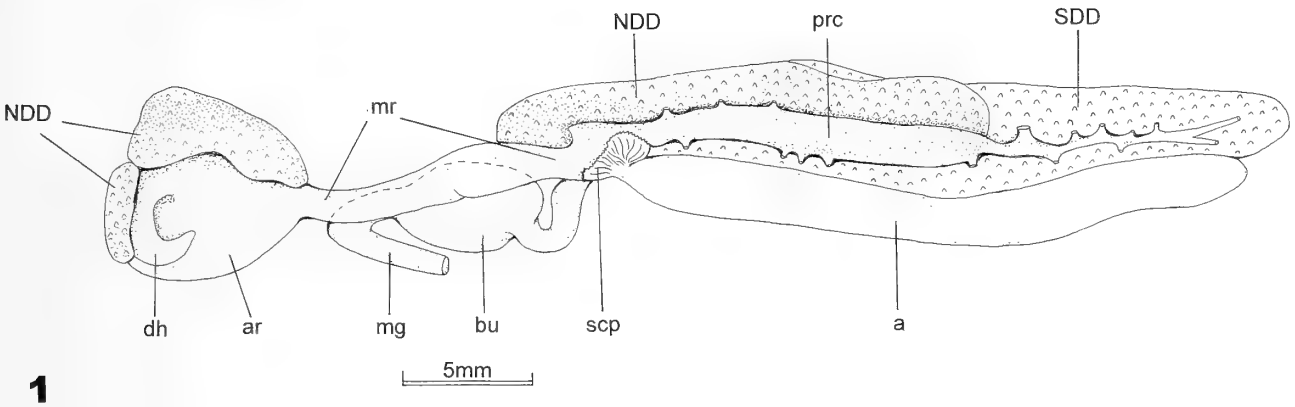
The relatively short and distally widened style-sac opens at the ventral wall of the globular region of the stomach, far from the opening of the intestine. The latter is located at the junction of the median and posterior region of the stomach. From its junction with the stomach, the style-sac extends to the right and ventralward until it makes contact with the sole of the foot. The area of contact can be identified externally as a lighter colored region at the right ventral quarter of the sole. A small baglike evagination (**ssa**) projects from the lateral surface, near the distal end of the style-sac (Figure 2). A similar baglike structure has been observed and received diverse denominations by different authors (Table 1). In *Nausitora fusticula* it is herein named the "appendix of the style-sac" following Lazier (1924).

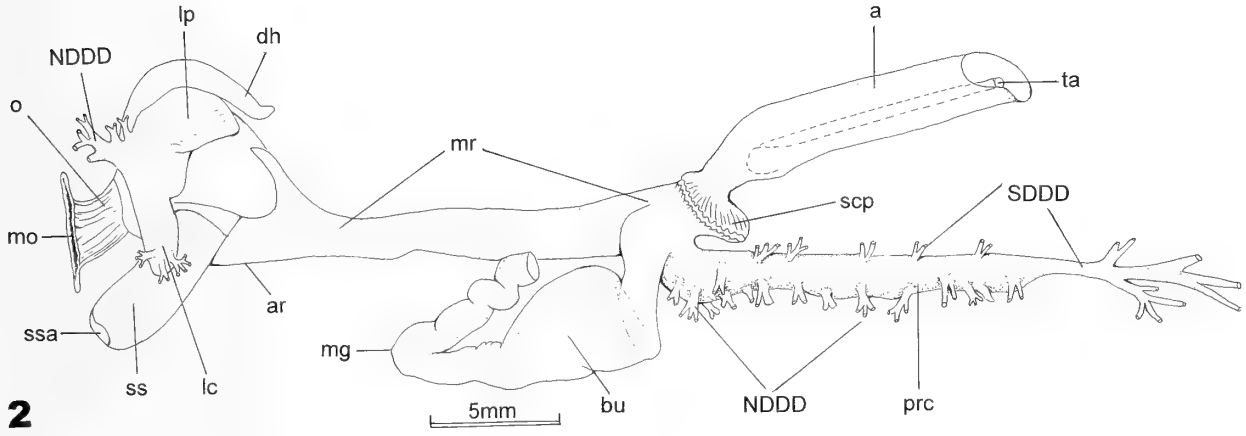
The dorsal hood is a small, conical pocket which extends from and over the left dorsal wall of the stomach, narrowing gradually as it curves postero-ventrally. The left pouch is a large, well-defined pocket located ventral to the dorsal hood (Figure 2), with a wide mouth at its junction with the stomach. The proximal end of the left pouch receives three ducts from the normal digestive diverticula (**NDDD**): one on the floor and two on the roof of this pocket. The latter two ducts have different diameters because one of them results from the convergence of several smaller ducts (Figure 2).

The cylindrical left caecum (Figure 2) projects from the floor of the stomach and passes ventrally to the right side onto the base of the style-sac. The left caecum receives four ducts from the **NDD** at its dorsal side, and two wide ducts from the specialized digestive diverticula (**SDD**) at its ventral side.

Nausitora fusticula possesses two right caeca: one anterior (**arc**), associated with the ventro-lateral wall of the globular part of the stomach (Figure 3), and one posterior (**prc**), far from the former, which opens at the distal end of the median region of the stomach (Figure 2). The anterior right caecum is a short swollen pocket which receives about 10 ducts from the **NDD** on its dorsal and ventral walls, and one large duct from the **SDD** on its ventral wall.

The median region of the stomach has a smooth external wall which gives rise to no structures, and receives no ducts from the digestive diverticula. The posterior region of the stomach comprises the posterior right caecum and the appendix (**a**). The posterior right caecum is a





Explanation of Figures 1 and 2

Nausitora fusticula. Figure 1. External dorsal view of the stomach and proximal region of the mid-gut after partial, removal of the digestive diverticula to expose the posterior right caecum. Figure 2. External ventral view of the stomach and initial region of the mid-gut after removal of the digestive diverticula. **a,** appendix (posterior third removed in Figure 2); **ar,** anterior region of the stomach; **bu,** bulbous region of the mid-gut; **dh,** dorsal hood; **lc,** left caecum; **lp,** left pouch; **mg,** mid-gut; **mo,** mouth; **mr,** median region of the stomach; **NDD,** normal digestive diverticula; **NDDD,** ducts from the normal digestive diverticula; **o,** esophagus; **prc,** posterior right caecum; **scp,** semi-spiral conical projection; **SDD,** specialized digestive diverticula; **SDDD,** ducts from the specialized digestive diverticula; **ss,** style-sac; **ssa,** appendix of the style-sac; **ta,** typhlosole of the appendix.

long, irregular cylindrical structure which opens into the median region of the stomach via a large and simple orifice. This caecum extends in a posterior direction, parallel to and near the mid-longitudinal line of the animal, and is entirely enveloped by the digestive diverticula, which are thicker around the right and ventral regions of the caecum. Approximately 15 ducts from the **NDD** open at the right wall (**NDDD**), and about five from the **SDD** open at the left wall of the posterior right caecum (**SDDD**). These ducts are all very short and branch soon after leaving the caecum. The distal end of this caecum narrows abruptly and links with a long, wide duct coming from the **SDD.** This duct gives rise to secondary ducts along its entire length, and the whole structure may easily be confused with a natural continuation of the caecum (Figures 1, 2).

The appendix is an extremely elongate semi-cylindrical pouch about one and a half times larger than the posterior right caecum, both in diameter and length. The appendix runs parallel to and at the right side of the posterior right caecum before joining with an elaborate, large, internally folded structure lying at the distal end of the median re-

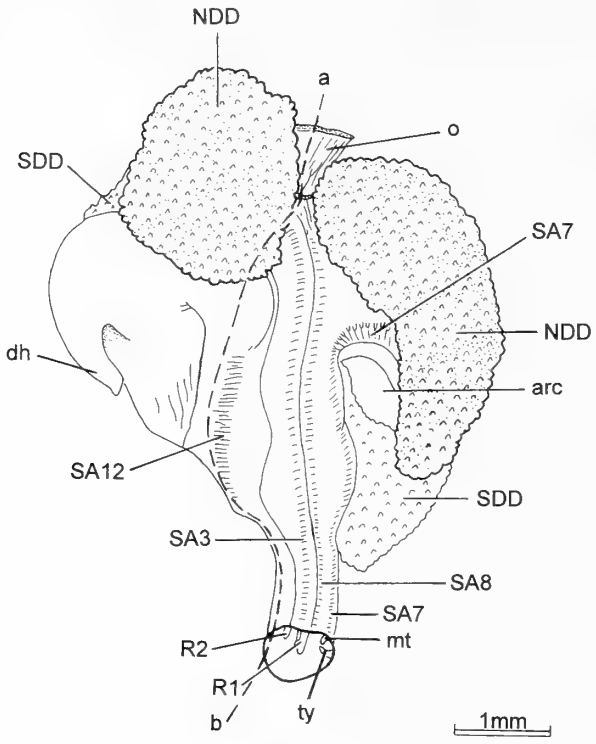


Figure 3

Nausitora fusticula. External dorsal view of the anterior, and part of the median regions of the stomach. Digestive diverticula partially removed to expose underlying structures. Internal structures are seen through the semi-transparency of the stomach wall. **arc,** anterior right caecum; **dh,** dorsal hood; **mt,** minor typhlosole; **NDD, SDD,** normal and specialized digestive diverticula, respectively; **o,** esophagus; **R1, R2,** folds of the stomach wall; **SA3, SA7, SA8, SA12,** sorting areas; **ty,** major typhlosole. "**a–––b**," line of incision to expose the internal structures shown in Figure 5.

gion of the stomach. Seen either from the left or the dorsal sides, this structure presents a corrugated external wall funneling off in the direction of the appendix. Seen from the right or the ventral sides, a similar corrugated wall is seen funneling off in the opposite direction. The whole structure has the aspect of two funnels joined together by their larger openings with an additional complexity: it bulges to the right in a conical fashion, turns ventrally at the same time it spirals, and partially embraces the proximal end of the appendix. This complex structure is herein named the "semi-spiral conical projection" (**scp**) (Figure 4).

The mid-gut leaves the distal end of the median region of the stomach, near and ventral to the opening of the appendix, and extends ventralward for a short distance, then turns abruptly forward and immediately swells to form a large bulbous region (Figures 1, 2, 4). As the mid-gut proceeds forward, it returns to its initial diameter, and shortly afterward curves to the left, then backward running ventrally to the stomach and appendix. At the distal end of the latter, the mid-gut makes a loop to run now in an opposite direction dorsally to the stomach. In its terminal part, the mid-gut passes first around the ventral, then the anterior side of the posterior adductor muscle and terminates at the anus on the dorsal side of this muscle. Inspection of the interior of the mid-gut reveals the presence of typhlosoles only within and near the vicinity of the bulbous swelling.

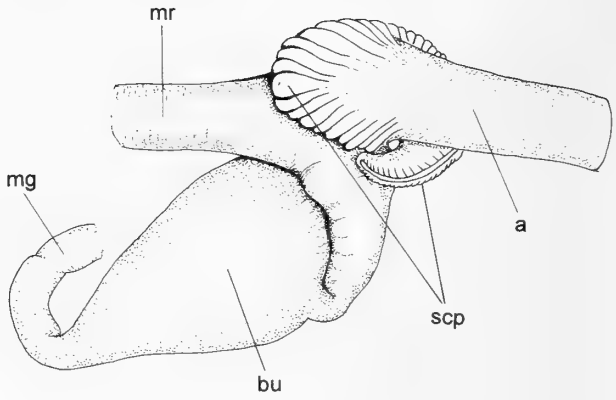


Figure 4

Nausitora fusticula. Left ventro-lateral view of a section of the stomach/appendix/mid-gut joining, to show the external appearance of the semi-spiral conical projection. **a,** appendix; **bu,** bulbous region of the mid-gut; **mg,** mid-gut; **mr,** median region of the stomach; **scp,** semi-spiral conical projection.

Internal Anatomy of the Digestive Tract

The internal anatomy of the digestive tract and respective ciliary currents of *Nausitora fusticula* are illustrated in Figures 5–11. The nomenclature used in the identification of structures is adopted from Purchon (1960).

The anterior, globular region of the stomach is shown in Figure 5. The inner wall of the esophagus (**o**) is longitudinally folded. Cilia on the wall impel particles entangled in a mucus strand toward the head of the crystalline style. Isolated particles on the left and dorsal side of the esophagus are deviated onto the dorsal hood by cilia on a wide and short fold (**R**).

The dorsal surface of the style-sac is longitudinally grooved. The crystalline style itself (**cs**) is short and pear-shaped. The part which projects into the stomach is more slender and has a distal tapering end. As inferred from the displacement of particles on the ciliated epithelium of the style-sac when dorsally observed, the style rotates in a clockwise direction.

The gastric shield (**gs**) is a saddle-shaped structure which lines a limited area of the left posterior corner of the stomach and partially embraces the opening of the style-sac. The antero-dorsal margin of the gastric shield

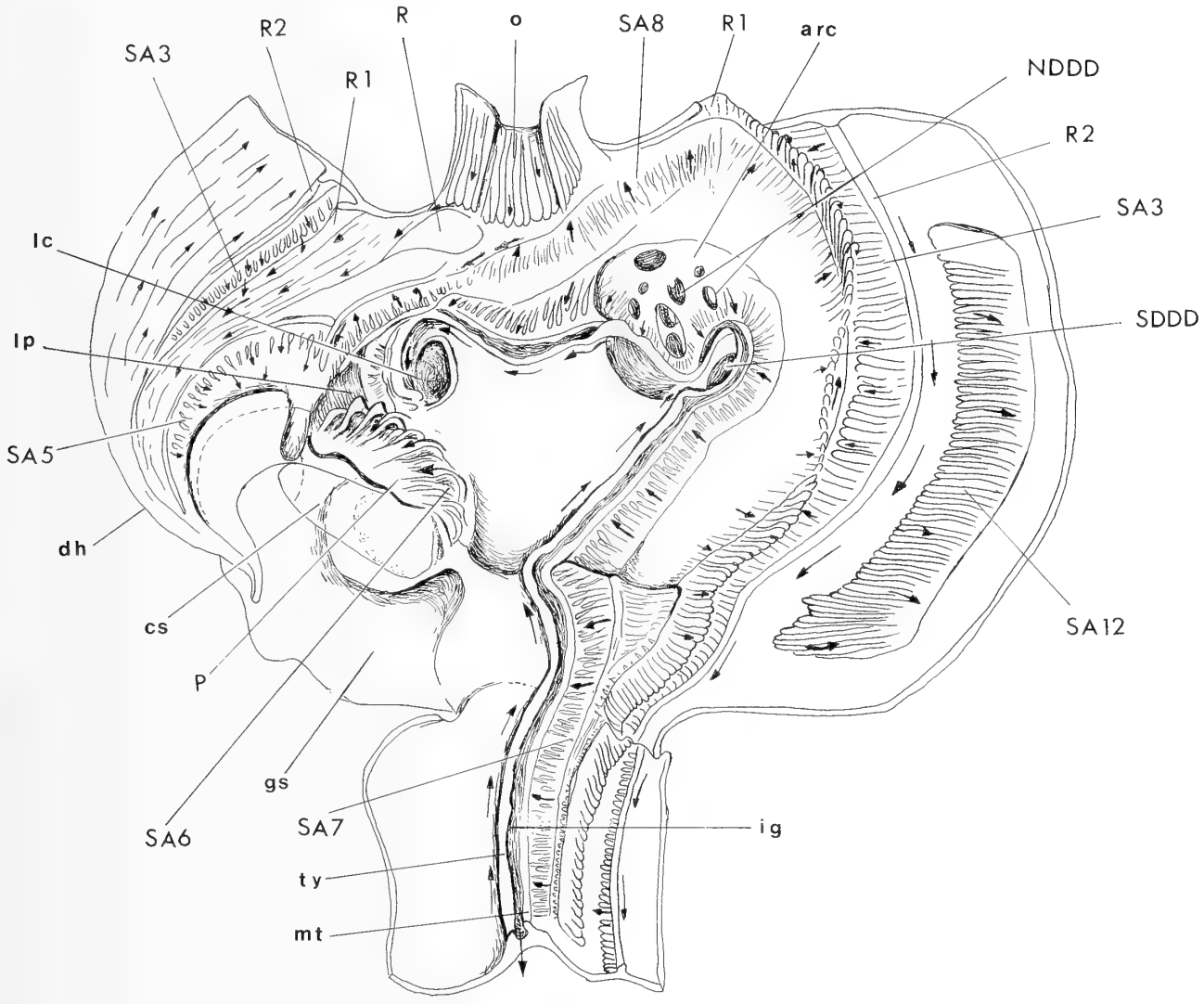


Figure 5

Nausitora fusticula. Internal anatomy of the anterior, and part of the median regions of the stomach, seen after being opened by an incision as indicated by the broken line "**a– – –b**" in Figure 3. **arc,** anterior right caecum; **cs,** crystalline style; **dh,** dorsal hood; **gs,** gastric shield; **ig,** intestinal groove; **lc,** left caecum; **lp,** left pouch; **NDDD, SDDD,** openings of ducts from the normal and specialized digestive diverticula, respectively; **mt,** minor typhlosole; **o,** esophagus; **P, R, R1, R2,** folds of the stomach wall; **SA3, SA5, SA6, SA7, SA8, SA12,** sorting areas; **ty,** major typhlosole.

gives off two V-shaped projections, one of which penetrates the dorsal hood, the other the left pouch.

The left pouch (**lp**) opens on the antero-lateral wall of the stomach through a wide orifice interposed between that of the dorsal hood, dorsally, and that of the left pouch, ventrally. A well-developed sorting area (**SA6**) of fine transverse folds and grooves extends across the roof and part of the floor of this pocket. On the roof and in intimate contact with **SA6** there are also openings of two ducts coming from the **NDD**. Another duct from the **NDD** opens at the floor of the left pouch, separate from **SA6**. This sorting area extends from the roof of the left pouch and lines the anterior surface of a broad prominence (**P**) which projects from the median line of the stomach floor. The prominence partially isolates the head of the crystalline style within the general cavity of the stomach. The transverse folds of **SA6** become taller and longer on the surface of the fleshy fold; ciliary currents on them carry particles dorsalward to be caught by the head of the rotating style.

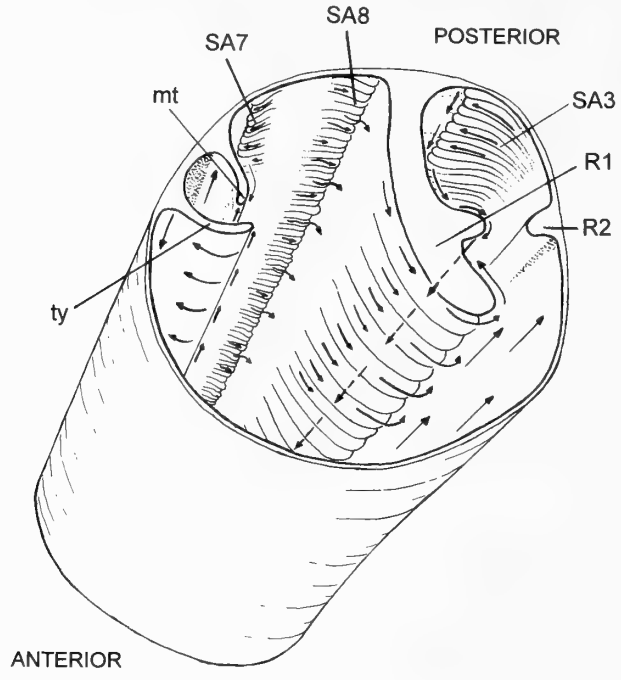


Figure 6

Nausitora fusticula. Diagram of a section of the median region of the stomach, and respective ciliary mechanisms. **mt,** minor typhlosole; **R1, R2,** folds of the stomach wall; **SA3, SA7, SA8,** sorting areas; **ty,** major typhlosole.

The conical-shaped dorsal hood (**dh**) has its postero-ventral wall protected by a long wing of the gastric shield. On its roof a transversely folded sorting area (**SA3**), flanked by two conspicuous folds (**R1, R2**), extends to the right side, passes dorsally to the esophagus opening, and extends backward until it terminates inside the semi-spiral conical projection around the opening of the appendix (Figures 5–7). Cilia on **SA3** beat along the grooves and folds, moving particles onto the base of **R1**. At the ventral edge of the mouth of the dorsal hood, another long, transversely folded sorting area (**SA8**) begins. It passes ventrally to the esophageal opening, then joins with and runs parallel to the fold **R1** and ends just before the opening of the posterior right caecum (**prc**). This sorting area is not as evident along the median region of the stomach as it is in the anterior region of the organ. On the section of **SA8** which lies at the vicinity of the esophageal orifice and dorsal hood, particles are carried forward along the folds and grooves. At the anterior edge of **SA8** these particles are deviated to the left by a feeble longitudinal tract of cilia, then onto the crystalline style. The remaining region of **SA8** running throughout the median region of the stomach (Figures 6, 7) conducts particles onto **R1**.

The fold **R1** begins completely smooth and low inside the dorsal hood and grows higher, with one side deeply, transversely plicate, as it passes over the esophageal orifice and continues posteriorward. At the same time a longitudinal chord arises in the side facing **R2**. This chord delimits two distinct regions: a broader, smooth proximal one, and a narrower distal one. The latter is scalloped by the free rounded tips of the folds on the opposite face. As soon as **R1** penetrates the semi-spiral projection at the distal end of the median region of the stomach, it suddenly diminishes in height and complexity, and terminates as a thin blade. The fold **R2** is smooth throughout its extent, and lower than **R1**. The former lacks ciliary activity (Figures 5–7).

Particles carried on **SA8** in the median region of the stomach are conducted onto the folded surface of **R1** where very active cilia move them toward the rounded tip of the plica (Figure 6). From here, large particles are quickly captured by a strong ciliary current flowing backward on the stomach wall parallel to **R2**, and carried onto the appendix. Small particles arriving at the free tip of the folds are driven around the latter and transferred to the very active current along the longitudinal chord. From here these particles are conducted forward, back to the anterior region of the stomach.

Another slight transversely folded sorting area (**SA5**), restricted to the limits of the dorsal hood lies ventrally, parallel and adjacent to the wing of the gastric shield (Figure 4). Cilia on this area carry particles onto the wing of the gastric shield. The remainder of the surface of the dorsal hood, posterior to the fold **R2** is longitudinally striated; cilia on it conduct particles out of the dorsal hood. Another narrower area, lying anterior to **R1**, exhibits fine grooves and long, slender elevations. These exhibit developmental variation according to the individual. This narrow area helps transfer particles onto the dorsal hood.

The sorting area **SA3** is formed by simple, short, and low transverse folds, throughout its extent. As it reaches the anterior wall (anterior funnel) of the semi-spiral conical projection, some folds become very high, long, and intermingled with lower ones of variable lengths. This complexity is maintained as **SA3** narrows and goes deep into the distal free end of the conical projection (Figure 7). All along the extent of **SA3**, which lies within the median and anterior regions of the stomach, ciliary currents carry particles onto the base of **R1**. Here, they may be caught either by a weak longitudinal current running forward, toward the dorsal hood, or by cilia on the smooth face of **R1** and conducted onto the strong ciliary tract along the longitudinal chord present on this face of **R1**. This strong current also carries particles forward toward the dorsal hood.

The posterior wall of the semi-spiral conical projection contains a series of long, very elaborate fleshy folds which form the sorting area **SA11**. These folds are high and thick, with an intricate outline at their proximal part, adjacent to **R2**, and diminish in height and complexity as

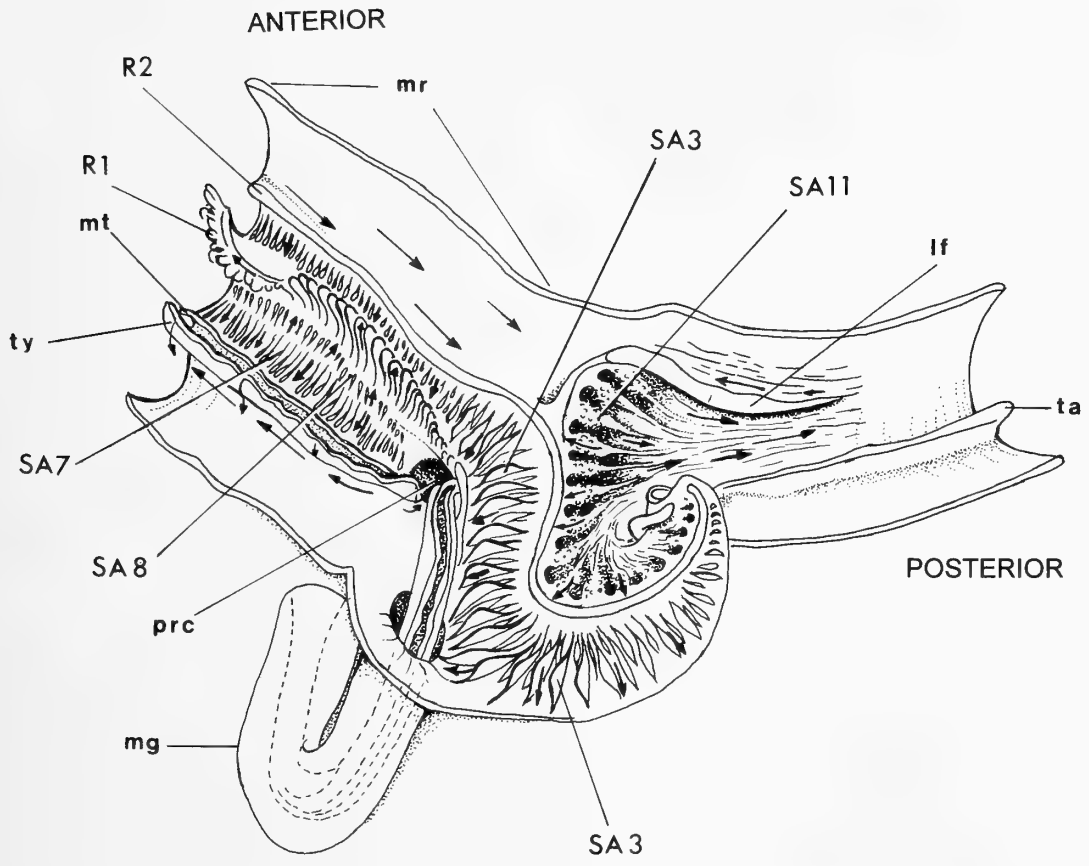


Figure 7

Nausitora fusticula. Internal view of a section of the stomach/appendix/mid-gut joining, to show their respective structures and main ciliary currents. **lf,** smooth longitudinal fold at the entrance of the appendix; **mg,** mid-gut; **mr,** median region of the stomach; **mt,** minor typhlosole; **prc,** opening of the posterior right caecum; **ta,** typhlosole of the appendix; **ty,** major typhlosole; **R1, R2,** folds of the stomach wall; **SA3, SA7, SA8, SA11,** sorting areas.

they extend shallowly into the appendix (**a**). One smooth longitudinal fold (**lf**), which is slightly longer than the folds of **SA11** limits this sorting area at the roof of the appendix. This fold, along with the typhlosole of the appendix, incompletely divides the opening of the appendix into two orifices. Particles carried toward the appendix along the active ciliary tract on the wall of the anterior and median regions of the stomach are submitted to the sorting mechanisms on **SA11**. Cilia on the folds of this sorting area direct large particles out of the appendix, throwing them over **R2**, then onto **SA3**. Small particles, however, fall into the grooves of **SA11** and finally enter the appendix. The fine longitudinally striated epithelium on the roof of the appendix near the opening slowly conducts particles out of the appendix.

The appendix (Figure 8) presents throughout its floor a fleshy fold, the typhlosole of the appendix, the free edge of which is irregularly swollen in live specimens and with brownish pigmentation internally. In prepared histological sections, the swollen free edge becomes arborescent in shape, as a result of dehydration (Figure 8B). The typhlosole of the appendix extends up to but does not fuse with the blind distal end of the appendix (Figure 8A). Cilia were not detected on the typhlosole of the appendix. This fold proved to be quite active, exhibiting wormlike movements in healthy specimens. Such movements may contribute effectively to moving the contents within the appendix.

The major typhlosole (**ty**), accompanied along its extent by the intestinal groove (**ig**) begins as a low fold at the initial section of the mid-gut, near but distally to the bulbous region (**bu**) of the latter (Figure 9A). A typhlosole is lacking all along the remaining part of the mid-gut. As the major typhlosole enters the bulb, it becomes very high and spirals in a counterclockwise direction. Before entering the stomach, it assumes its initial conformation. It was almost impossible to dissect the bulbous region and unroll the typhlosole without damage. Observation of ciliary currents on the latter was very difficult. The minor typhlosole (**mt**) arises within the bulb and runs

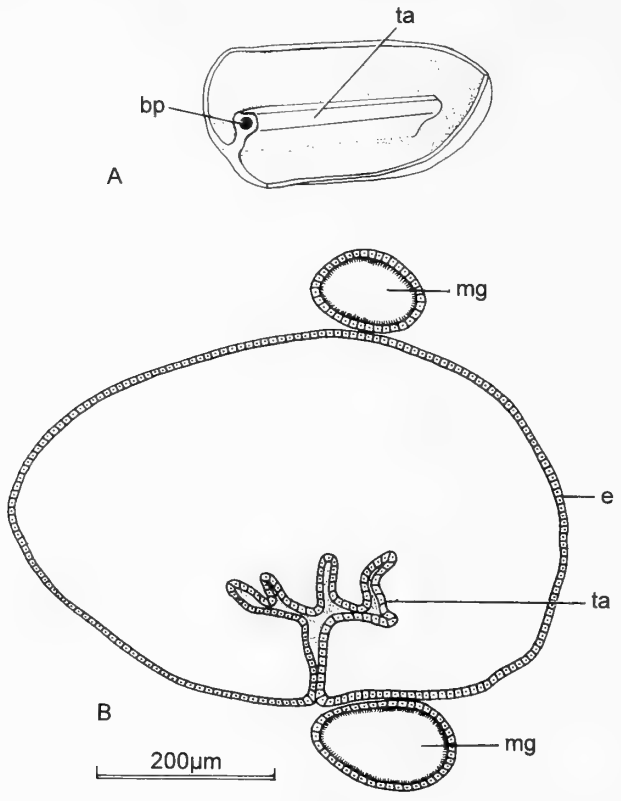


Figure 8

Nausitora fusticula. **A,** diagram of the dissected distal end of the appendix, to show its typhlosole as seen in live specimen. **bp,** brownish pigmentation within the typhlosole; **ta,** typhlosole of the appendix. **B,** transverse histological section of the appendix to show the arborescent appearance of its typhlosole after dehydration. **e,** epithelium of the appendix; **mg,** mid-gut; **ta,** typhlosole of the appendix.

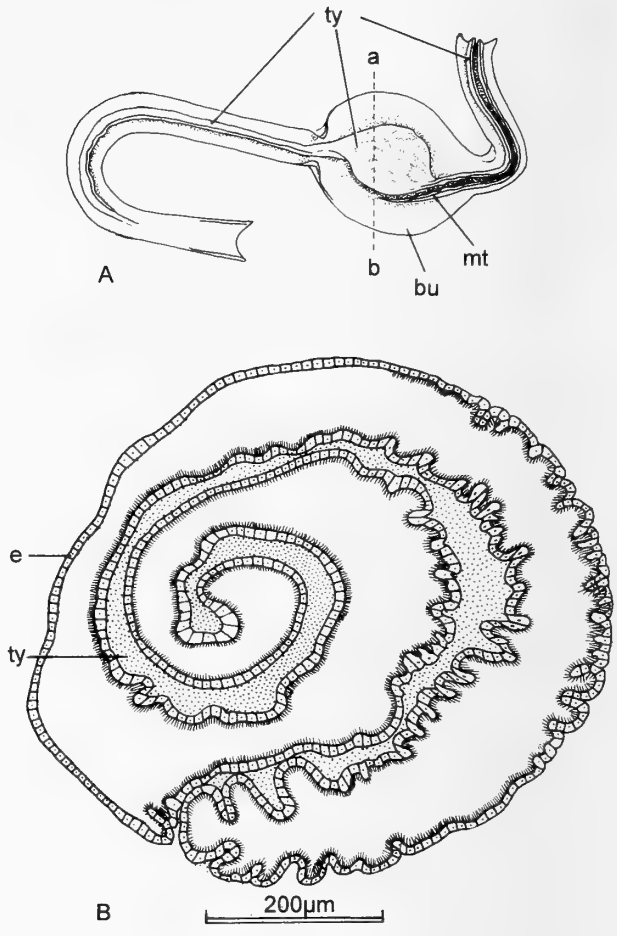


Figure 9

Nausitora fusticula. **A,** semi-diagrammatic drawing of the initial stretch of the mid-gut and respective bulbous region (**bu**), opened longitudinally to show the origin of the minor (**mt**) and major (**ty**) typhlosoles, and the greatly enlarged, spiraled region of the latter. **B,** transverse histological section through the bulbous region of the mid-gut (broken line "**a– – –b**" in **A**). **e,** epithelium of the bulbous region of the mid-gut; **ty,** major typhlosole.

parallel to the major typhlosole, flanking the intestinal groove along its entire course inside the stomach.

The typhlosoles emerge into the median region of the stomach and traverse the floor of this organ from the left to the right side and enter the posterior right caecum dorsally (**prc**) (Figures 7, 10). Here they penetrate deeply into the apex of the caecum, then return via its ventral wall. Within this pocket a finely striated area, which receives the ducts from the specialized digestive diverticula, borders the major typhlosole. The sorting area **SA7** runs parallel and adjacent to the minor typhlosole and flanks a smooth area which receives the majority of the ducts from the normal digestive diverticula related to the posterior right caecum. The remaining ducts from the **NDD** open adjacent to **SA7**. Neither typhlosole sends projections into any opening of these ducts. Ciliary currents on the right lateral wall of this caecum carry particles onto the distal end of this pocket where it links with the long wide duct from the **SDD.** Nevertheless, particles were never seen entering the orifice of this large duct or that of any duct which opens along the right lateral wall.

Particles arriving on **SA7** are sent toward the minor typhlosole, and either enter the intestinal groove to be rejected via the mid-gut, or follow a backward trajectory to travel along a feeble ciliary current on the free edge of both typhlosoles. After a short trajectory along these currents, such particles are thrown onto the outer face of the major typhlosole, then are carried transversely onto the base of this fold. There a strong longitudinal current carries them back to the general cavity of the stomach.

The typhlosoles, along with **SA7** (Figures 7, 10), emerge from the posterior right caecum and extend up to the anterior region of the stomach, running dorso-laterally along the left wall of the median region of the stomach

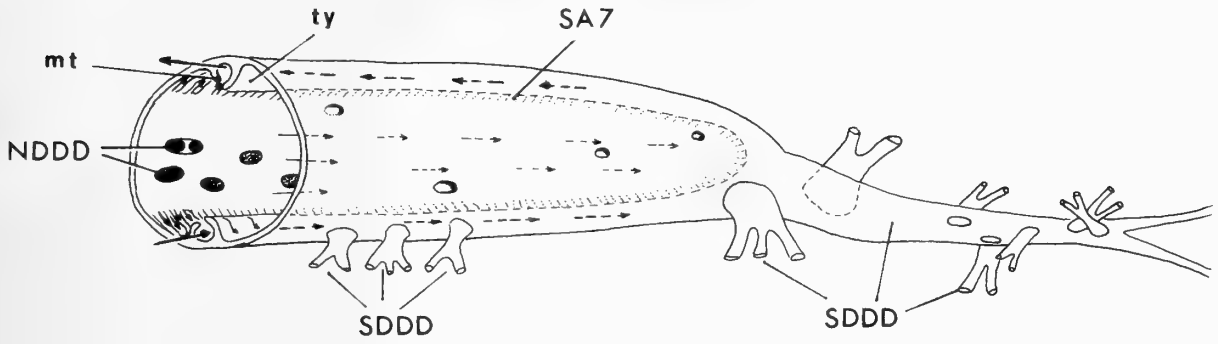


Figure 10

Nausitora fusticula. Semi-diagrammatic drawing of the distal end of the posterior right caecum. **mt,** minor typhlosole; **NDDD, SDDD,** ducts from the normal and specialized digestive diverticula, respectively; **SA7,** sorting area; **ty,** major typhlosole.

(Figures 5, 11). Within the anterior region of the stomach the typhlosoles enter the right caecum where they form a loop and separate two distinct areas. The first is a finely striated postero-ventral one, which receives a single wide duct from the **SDD** and some ducts from the **NDD.** The other is an antero-dorsal area, which contains a section of the sorting area **SA7,** wherein the remaining **NDDD** open. The major typhlosole does not send projections into the opening of any duct.

From the anterior right caecum, the typhlosoles along with **SA7** run transversely across the anterior floor of the stomach to enter the left caecum. This caecum opens into the floor of the stomach via a well-defined aperture, which is confluent with the wide, overhanging mouth of the left pouch. In their course toward the left caecum, the typhlosoles and **SA7** pass close to the opening of one duct from the normal digestive diverticula related to the left pouch, which is contiguous with the opening of the left caecum. In a very few specimens, the minor typhlosole and **SA7** penetrate slightly into the opening of this duct. The typhlosoles and **SA7** enter the left caecum, running along the anterior wall, and return along the posterior wall to terminate in a short semicircular loop at the mouth of this caecum (Figure 11B). In some specimens, these structures continue onto the apex and finish near it describing a complete spiral turn (Figure 11C). The typhlosoles rarely send a tongue into the mouth of the **NDDD** and **SDDD** related to the left caecum. Some specimens exhibited slight penetration of the minor typhlosole and accompanying **SA7** into an opening of a duct from the **NDD,** which lies near the aperture of the left caecum (Figure 11C). Similar to what was observed for the two right (anterior and posterior) caeca, the openings of the ducts of the **SDD** within the left caecum are associated with the finely striated areas at the vicinity of the major typhlosole.

The sorting area **SA7** has conspicuous transverse folds in its section within the posterior right caecum and within the anterior globular region of the stomach. Along the median region of this organ this area is sometimes conspicuous in certain individuals, but barely discernible in others. Ciliary currents present on **SA7,** as well as on both typhlosoles and associated intestinal groove, follow the same pattern already described for these structures within the posterior right caecum.

Beginning at the mouth of the dorsal hood and extending all along the roof of the anterior region of the stomach there is a sorting area (**SA12**) (Figure 5). It consists of a long series of fine ridges and grooves which run at a right angle to the fold **R2.** Cilia on **SA12** send particles onto the head of the crystalline style.

DISCUSSION

Comparison of variation in the structures of the stomach of teredinids and correspondence among structures described by different authors, under different names, are set out in Table 1. Several are discussed individually below.

The very elongate and highly modified stomach of *Nausitora fusticula* reveals the consequences of the evolutionary trends observed in the teredinids toward the deep boring mode of life, with corresponding utilization of wood as a food source. This organ is highly modified when compared with the typical globular lamellibranch stomach in all the species studied by Purchon (1956, 1957, 1958, 1960), except the Teredinidae analyzed by Purchon (1960). Its extension well beyond the posterior adductor muscle is a character which allows it to be classified as a type III stomach (elongate) of Turner (1966).

Considering the internal anatomy of the stomach of *N. fusticula,* the presence of the intestinal groove accompanying the major typhlosole as it forms a circular flange, which passes into the right caecum, and another which similarly passes into the left caecum, allows the classifi-

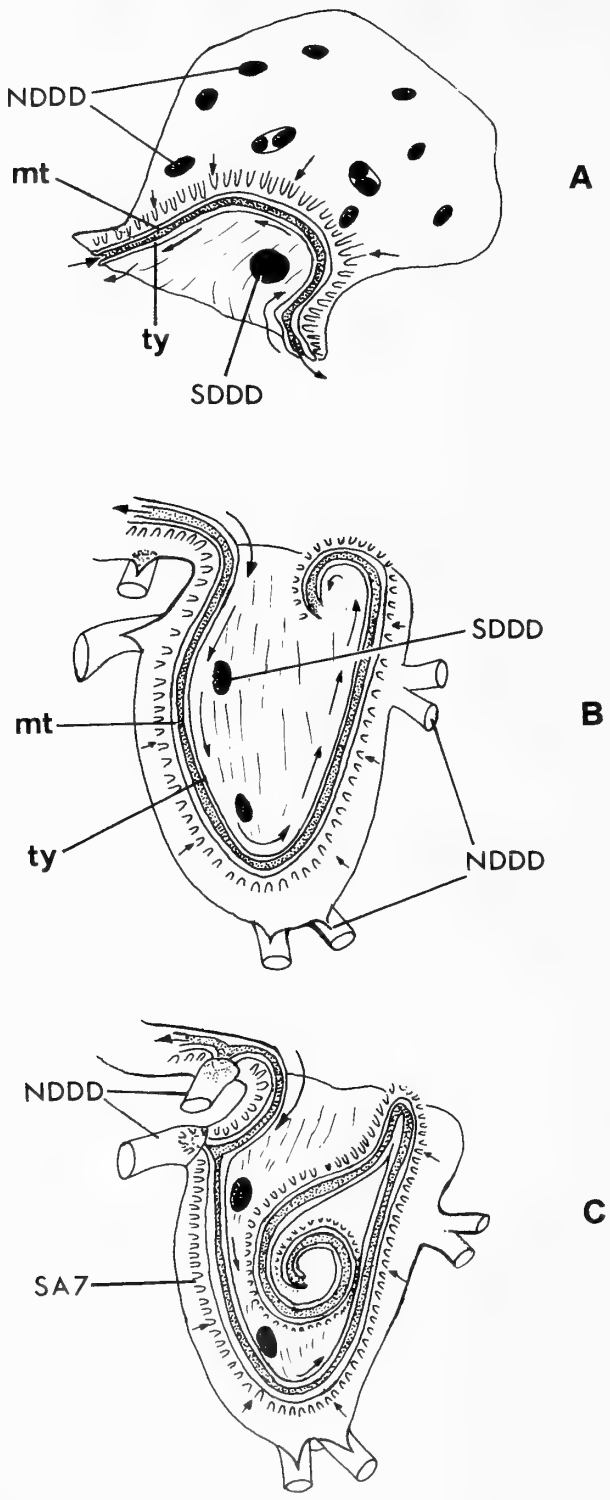


Figure 11

Nausitora fusticula. Semi-diagrammatic representation of the anterior right caecum (**A**), and left caecum (**B,C**). The latter two figures show variations in the route of the typhlosoles and **SA7;** **mt**, minor typhlosole; **NDDD, SDDD,** ducts from the normal and specialized digestive diverticula, respectively; **SA7,** sorting area; **ty,** major typhlosole.

cation of this stomach as a type V of Purchon (1960, 1990).

Among the teredinid species which have elongate stomachs, the right caecum is known always to be posteriorly located. Purchon (1960) interpreted this configuration as a consequence of the lengthening of the stomach, with corresponding displacement of the typical right caecum to the posterior region of the organ. *Nausitora fusticula* shares this characteristic since it has a well-developed posteriorly located right caecum. Nevertheless, this species also possesses a swollen and short pocket, which emerges from the right side of the anterior globular region of the stomach and receives ducts coming from both the **NDD** and **SDD.** This pocket is also invaded by the major typhlosole. Typically, this pocket is the right caecum of a type V stomach of Purchon (1960), and seems to be homologous with the right caecum found in species with a globular type of stomach as indicated by its position and organization. Thus, the presence of two right caeca characterizes the stomach of *N. fusticula* as a variation of the type V stomach of Purchon (1960). Only one posteriorly located right caecum occurs in the stomach of *Teredo navalis* (Lazier, 1924; Morton, 1970; Martinez, 1987), and probably in *Nausitora hedleyi* and *Teredo furcifera* studied by Saraswathy & Nair (1971). These last two authors did not supply convincing elements to interpret the existence of an anterior right caecum in the Teredinidae they studied. *Nausitora fusticula* is the only known species of Teredinidae to present two right caeca.

In *Nausitora fusticula* the **NDD** and **SDD** open into the stomach through separated ducts, as Morton (1970) also described for *Teredo navalis.* Potts (1923), Lazier (1924), and Saraswathy & Nair (1971), however, mentioned that in the species they studied, the **SDD** and **NDD** open into the stomach by common ducts.

In *Nausitora fusticula* the ducts coming from the **NDD** open exclusively into the left pouch, left caecum, and both anterior and posterior right caeca. Those coming from the **SDD** open exclusively into the three caeca where their openings are segregated from the **NDDD** openings by the typhlosoles. The **SDDD** openings are always alongside the major typhlosole, while the **NDDD** openings exist alongside the minor typhlosole and accompanying sorting area **SA7.** Lazier (1924) and Martinez (1987) referred to the presence of four main ducts from the **SDD** joining with the median region of the stomach of *Teredo navalis.* The openings of such ducts were identified by Morton (1970) as "lateral caeca."

Sawdust suspension or the mixture of this material with

Acquadag and carmine precipitated at different regions of the stomach of *Nausitora fusticula* were not adequate to detect ciliary tracts specialized to deal with wood fragments. Even the finest fragments of wood that we had obtained were not as small as those found in the appendix, and were not carried by the cilia of the stomach. This observation suggests that the sorting areas are adapted to deal only with very small wood fragments. All attempts to visualize the entrance of any kind of particle into the ducts of the **SDD** and **NDD** failed. Only cleansing ciliary currents were observed around such openings, similar to what Purchon (1955) reported in members of the Pholadidae. Thus, the mechanisms which operate inside the stomach of *N. fusticula* to select wood fibers and filtered suspension were not revealed, which validates the statement of Lazier (1924) that "the method of manipulating the wood chips which are ingested would of itself be an interesting discovery." It also remains uncertain if the wood fibers and filtered suspension simultaneously enter the mouth of the animal and are concomitantly selected within the stomach, or if they enter at different times. Furthermore, it is still undetermined if sorting is a temporal as well as a mechanical process, as suggested by Morton (1970, 1978). Turner (1984) stated that the Teredinidae do not interrupt the process of filtering plankton to dig wood, and vice versa as maintained by Morton (1970, 1978), and that these two activities are executed concomitantly. Lopes & Narchi (1998) observed that particles added at the same time on the foot epithelium and ctenidia of *N. fusticula* were simultaneously selected and transported to the mouth for ingestion.

The caeca of the stomach of *Nausitora fusticula* probably have the main responsibility for the final separation of minute wood fibers and filtered suspension before they are passed to their appropriate digestive diverticula. Purchon (1955) invoked volumetric alteration of the stomach as the mechanism by which particles pass into the ducts of the digestive diverticula. Nevertheless, Morton (1970) observed particles entering by ciliary action into the **SDDD** and **NDDD** of *Teredo navalis* and *Lyrodus pedicellatus.* He interpreted the development of **SDDD** on the "left" side of the major typhlosole of both species as an evolutionary specialization for the collection and utilization of large particles; in typical eulamellibranchs these would be swept over the major typhlosole from the left to right side to be voided via the intestinal groove. "This adaptation has complicated the sorting function, ancestral cleansing currents directing wood fragments into the ducts on the floor of the caeca," concluded Morton (1970).

Purchon (1941, 1955) showed that the appendix of the Adesmacea (Pholadidae, Xylophaginidae, and Teredinidae) are structurally and functionally similar to the "postero-dorsal caecum" discovered and described by Yonge (1949) for the Tellinacea. Based upon this, Purchon (1941, 1955) concluded that these structures are homologous and provide reliable evidence of a relationship between these groups. This conviction led Purchon (1960) to predict the occurrence of a particular sorting area (**SA11**) associated with the mouth of the appendix also in members of the Adesmacea in which an appendix is present. This sorting area was found only in *Asaphis* (Psammobiidae, Tellinacea) among the Tellinacea and Adesmacea studied by Purchon (1960).

The complex semi-spiral conical projection identified in association with the aperture of the appendix of *Nausitora fusticula* bears a typical sorting area. This surely corresponds to **SA11** in the concept of Purchon (1960). Its occurrence in *N. fusticula* confirms Purchon's prediction about the existence of this area in the Adesmacea. It also provides new data in support of his hypothesis regarding the homology between the appendix of the Adesmacea and the "postero-dorsal caecum" of the Tellinacea.

Quatrefages (1849), Lazier (1924), Rancurel (1971), and Saraswathy & Nair (1971) referred to the existence of a folded structure around the opening of the appendix into the stomach in the teredinids they studied. Saraswathy & Nair (1971) described up to nine longitudinal folds just anterior to the appendix opening into the stomach of *Nausitora hedleyi.* Such structures could correspond to the area **SA11** of *N. fusticula.* Purchon (1960), in *Psiloteredo amboinensis,* and Morton (1970), in *Teredo navalis,* described small conical projections around the opening of the appendix, the function of which is not known.

Morton (1970) stated that the elongation of the stomach also resulted in the elongation of the major typhlosole, and of the ridges **R1** and **R2.** The ridge **R1** in *N. fusticula* differs greatly from its homologue in other teredinids by its transversely folded surface acting as a sorting area. Morton (1970) related these two ridges to the transport of particles to and from the sorting area **SA3** and the dorsal hood.

In *Teredo navalis* and *Lyrodus pedicellatus* the sorting area **SA3** was evolutionarily removed from its original place in the dorsal hood to the aperture of the appendix (Morton, 1970). In *Nausitora fusticula* this sorting area runs from its origin within the dorsal hood, throughout the entire extent of the anterior and median regions of the stomach and terminates within the semi-spiral conical projection. Similarly, the sorting areas **SA7** and **SA8** in *N. fusticula* largely exceed the extension of their homologues in the stomach of *Psiloteredo amboinensis* and *Teredo navalis* studied by Purchon (1960) and Morton (1970), respectively. In these last species, **SA7** is confined to the stomach wall under the esophageal orifice, and **SA8** to the dorsal hood. As in the preceding species, the area **SA6** in *N. fusticula* extends to the right on the fold **P.**

Besides the above-mentioned areas, the stomach of *N. fusticula* also bears the sorting areas **SA5, SA11,** and **SA12.** Purchon (1960) considered **SA5** to occur sporad-

Table 1

Analyses of variation in the structures of the terredinids' stomach and correspondence among structures described under different names. Purchon's (1960) nomenclature and respective abbreviations constitute the basis for comparisons.

Stomach characteristics and alternative terminologies	*Teredo navalis* (3)(4)(6)(9)	*Lyrodus pedicellatus* (6)	*Psiloteredo amboinensis* (4)	*Teredo manni* (4)	*Teredo petiti* (7)	*Teredo adami* (7)	*Teredora princesae* (8)	*Teredo furcifera* (8)	*Nausitora hedleyi* (8)	*Teredo fatalis* (1)	*Xylotrya gouldi* (2)	*Bankia minima* (5)	*Nausitora fusticula* (10)
	T	T	T	T	T	T	T	T	B	B	B	B	B
Stomach type													
II (globular) of Turner, 1966			+	+	+	+	+			?			
III (elongate) of Turner, 1966	+	+						+	+	?	+	+	+
V of Purchon, 1960	+	+	+	+	+	+	?	?	+	?	?	?	+
A, Appendix (4)(6)(8)(9)(10) [= stomach caecum (1) = caecum of stomach (2) = caecum (3)(5) = gastric caecum (7)]	+	+	+	+	+	+	+	+	+	+	+	+	+
CP;CP′, Conical protuberances on appendix (4)(6)	+	+	+	–	?	?	?	?	?	?	?	?	–
DH, Dorsal hood (4)(6)(9)(10) [= secondary caecum of stomach (2) = dorsal caecum (3)(8) = "colimaçon" (7)]	+	+	+	+	+	+	+	+	+	?	?	?	+
LB, striated longitudinal band in the appendix (4)	–	–	+	+	?	?	?	?	?	?	?	?	–
LC, Left caecum (4)(6)(9)(10) [= left lateral caecum (7)]	+	+	+	+	+	+	?	?	+	?	?	?	+
LP, Left pouch (4)(6)(9)(10) [= lateral pouch (3)(8)]	+	+	+	+	?	?	+	+	+	?	?	?	+
MT, Minor typhlosole													
• ending near the mid-gut opening in the stomach (4)			+	+	?	?	?	?	?	?	?	?	
• accompanied the entire extent of the major typhlosole inside the stomach (10) [= T4 (9)]					?	?	?	?	?	?	?	?	+
P, Prominence on floor of the stomach, or shield shaped prominence (4)(6)(10)	+	+	+	+	?	?	?	?	?	?	?	?	+
RC, Right caecum													
• anteriorly located in type II stomach of Turner (4) [= right lateral caecum (7)]			+	+	+	+	?			?			
• anteriorly located in type III stomach of Turner [= anterior right caecum (10)]	–	–						–	–	?	?	?	+
• posteriorly located in type III stomach of Turner (4)(6)(9) [= posterior liver (3) = large digestive diverticle duct (2)(5)(8) = posterior right caecum (10)]	+	+						+	+	?	+	+	+
R, Ridge passing from the dorsal hood to the esophageal orifice (4)(10)	–	–	+	+	?	?	?	?	?	?	?	?	+
R_1, Ridge on the posterior wall of the dorsal hood													
• in type II stomach of Turner (4) [= fold 3 (7)]			+	+	+	+	?			?			
• extending up to the posterior right caecum opening in type III stomach of Turner (6)(10) [= gastric typhlosole (3)(8) = T_2(9)]	+	+						+	+	?	?	?	+
R_2, Ridge on the posterior wall of the dorsal hood													
• in type II stomach of Turner (4) [= fold 2(7)]			+	+	+	+	?			?			
• extending to the appendix opening in type III stomach of Turner (6)(10) [= low ciliated fold parallel to the gastric typhlosole (3) = ciliated ridge (8) = T_3 (9)]	+	+						+	+	?	?	?	+
SA_3, Principal sorting area of the dorsal hood													
• in type II stomach of Turner (4)			+	+	?	?	?			?			
• restricted to the opening of the appendix (6); extending from the dorsal hood to the appendix opening (10) in type III stomach of Turner	+	+						?	?	?	?	?	+

Table 1

Continued.

Stomach characteristics and alternative terminologies	*Teredo navalis* (3)(4)(6)(9)	*Lyrodus pedicellatus* (6)	*Psiloteredo amboinensis* (4)	*Teredo manni* (4)	*Teredo petiti* (7)	*Teredo adami* (7)	*Teredora princesae* (8)	*Teredo furcifera* (8)	*Nausitora hedleyi* (8)	*Teredo fatalis* (1)	*Xylotrya gouldi* (2)	*Bankia minima* (5)	*Nausitora fusticula* (10)
	T	T	T	T	T	T	T	T	B	B	B	B	B
SA_5, The sorting area on the posterior wall of the dorsal hood (10)	−	−	−	−	?	?	?	?	?	?	?	?	+
SA_6, The sorting area of the left pouch (4)(6)(10)	+	+	+	+	?	?	?	?	?	?	?	?	+
SA_7, Sorting area below the esophageal orifice (4)(6); accompanied the typhlosoles throughout their extent inside the stomach (10)	+	+	+	+	?	?	?	?	?	?	?	?	+
SA_8, Sorting area on the anterior roof of the stomach (4)(6); extending up to the posterior right caecum opening (10)	+	+	+	+	?	?	?	?	?	?	?	?	+
SA_{11}, Sorting area in the mouth of the appendix (10)	−	−	−	−	?	?	?	?	?	?	?	?	+
TA, Typhlosole in the appendix (4)(6)(8)(10) [= complex typhlosole (2) = fold 5 (7) = typhlosole (5)]	+	+	+	+	+	+	+	+	+	?	+	+	+
TY, Major typhlosole (4)(6)(10) [= gastrointestinal typhlosole (3)(8) = typhlosole (2)(5) = fold 1 (7) = T_1 (9)]	+	+	+	+	+	+	+	+	+	?	+	+	+
TY, Major typhlosole entering style-sac (6)	+	+	−	−	?	?	?	?	?	?	?	?	−
Dorsal chamber of the stomach (8)	−	−	−	−	−	−	−	+	−	?	−	−	−
Flap accompanied the "TY" and covered the intestinal groove in the left caecum and in the stomach (4)	−	−	−	+	−	−	−	−	−	?	?	?	−
Lateral caeca in type III stomach of Turner (6)(9) [= small orifices of the ventral livers (3)]	+	+						?	?	?	?	?	−
Semi-spiral conical projection (10)	−	−	−	−	−	−	?	?	?	?	?	?	+
Sorting area along the roof of the anterior region of the stomach [**SA12**] (10)	−	-	−	−	?	?	?	?	?	?	?	?	+
Typhlosole sac (6) [= vermiform tube of the style sheath (2) = tubular prolongation (5) = vermiform caecum (7) = appendix of the style-sac (3)(8)(10)]	+	+	−	−	+	+	+	+	+	?	+	+	+

(**T**) Teredininae and (**B**) Bankiinae, based on Turner (1966). Specific names follow the authors below mentioned. For an up-to-date specific nomenclature, see the "Introduction" of the present paper.

(+) Indicates presence, and (−) absence of the structure.

(?) Signifies unknown, or difficult to interpret from the description or illustration given by the author(s) below mentioned.

(1) Quatrefages (1849), (2) Sigerfoos (1908), (3) Lazier (1924), (4) Purchon (1960), (5) Bade et al. (1964), (6) Morton (1970, 1978), (7) Rancurel (1971), (8) Saraswathy & Nair (1971), (9) Martinez (1987), (10) Present paper.

ically in bivalves with type V stomachs, having been recorded only in Corbiculidae, Isocardiidae, Mactridae, Mesodesmatidae, Tellinidae, Solenidae, and Myidae. The descriptions and illustrations given by Lazier (1924), Purchon (1960), Morton (1970), and Martinez (1987) confirm the lack of those three areas in the stomachs of the species they studied. The same is not true for the species studied by Quatrefages (1849), Sigerfoos (1908), Bade et al. (1964), Rancurel (1971), and Saraswathy & Nair (1971) since the descriptions given by these authors are not sufficient to identify the presence of those areas. Thus, the record of **SA5, SA11,** and **SA12** in the stomach of *N. fusticula* is the first for the teredinids.

All the sorting areas described for the stomach of *N. fusticula,* except **SA12,** are homologous to the corresponding areas described by Purchon (1956, 1957, 1958, 1960). Since Purchon's terminology was adopted in the present work, and he described only the areas **SA** and

SA1 to **SA11** in the stomachs he studied, the newly described sorting area in *N. fusticula* was identified as **SA12.**

The presence of seven well-defined sorting areas on the stomach walls of *Nausitora fusticula,* and of the extensive folded surface of **R1** reveals specialization of the organ to deal with a great variety of isolated particles. It confirms the prediction made by Lopes & Narchi (1998) about the role of the stomach of this species in reference to the low selectivity exercised by the ctenidia and the very reduced labial palps.

The major typhlosole and the intestinal groove in *Nausitora fusticula* are peculiarly accompanied all along their course within the stomach by the minor typhlosole and the sorting area **SA7**; all these structures enter the left caecum where they terminate. In *Teredo manni,* Purchon (1960) described the intestinal groove as being protected by a "flap" which accompanied the major typhlosole in the left caecum and in the stomach, while the minor typhlosole is shown to enter the stomach and end at the vicinity of the opening of the appendix. Lazier (1924) and Martinez (1987) stated that the major typhlosole in *Teredo navalis* enters and finishes inside the left caecum, as is usual for the teredinids. Nevertheless, Morton (1970), while studying this same species, described and illustrated the major typhlosole leaving the left caecum as a very fine ridge which enters the style-sac. Within the style-sac, the major typhlosole forms a gutter and terminates as a small sac, which Morton (1970) termed the "typhlosole sac." *Nausitora fusticula* similarly has the style-sac longitudinally grooved and a baglike evagination at its distal end; however, the major typhlosole does not enter the style-sac.

Despite the great development of the appendix of *Nausitora fusticula* in relation to other stomach structures, that pocket is of a moderate size compared to the length of the animal. Its corresponding typhlosole of the appendix seems to be non-homologous with any fold in the stomach and mid-gut, because it begins inside the semispiral conical projection and ends inside the blind distal end of the appendix. Morton (1970) described the typhlosole of the appendix of *Teredo navalis* as a fleshy, coiled fold [= minor typhlosole (Morton, 1978)] which originates on the roof of the mid-gut and enters the appendix, then doubles back on itself, and terminates just within the opening of the pocket.

The slightly elevated typhlosole of the appendix of *Nausitora fusticula* has the same degree of development and arborescent free edge in histological preparations as that depicted by Sigerfoos (1908) in *Xylotrya gouldi* and by Bade et al. (1964) in *Bankia (Bankiella) minima.* It is comparatively more developed than its homologue in *Teredora princesae* studied by Saraswathy & Nair (1971), but weakly developed and lacking two-coiled lateral projections when compared to the typhlosole of *Teredo navalis* studied by Lazier (1924), and those of *Nausitora hedleyi* and *Teredo furcifera* studied by Saraswathy & Nair (1971).

The selective action exerted by the area **SA11** which conducts only minute particles of carmine and Acquadag into the appendix of *Nausitora fusticula* provides indirect evidence that this sorting area is mainly responsible for the sorted wood observed within the appendix. Wood fragments may be kept in motion within the appendix under the action of the typhlosole of the appendix, which exhibits wormlike undulations in healthy specimens.

In *Nausitora fusticula* the typhlosole of the appendix is not ciliated. Lazier (1924) and Morton (1970) described the same for *Teredo navalis,* Saraswathy & Nair (1971) for *Nausitora hedleyi* and *Teredo furcifera,* and Bazylinski & Rosenberg (1983) for *Teredo bartschi* Clapp, 1923, and *Bankia setacea* (Tryon, 1863). Cilia were reported for the typhlosole of the appendix of *Xylotrya gouldi* by Sigerfoos (1908), *Bankia minima* by Bade et al. (1964), and *Teredora princesae* by Saraswathy & Nair (1971).

It was impossible to demonstrate peristaltic movement of the appendix walls of *Nausitora fusticula,* which Purchon (1960) considered responsible for returning the material stored in the appendix of *Psiloteredo amboinensis* back into the stomach.

Centripetal compressions transmitted from the contracted mantle onto the visceral mass could operate in *Nausitora fusticula* to force wood out of the appendix. Another possibility is that this transference is produced only by the feeble ciliary activity detected on the fine, longitudinally striated epithelium which lines the roof of the appendix opening.

The strong inward ciliary activity of **SA11** and the feeble outward currents on the roof of the appendix may largely contribute to a long persistence of wood within the appendix, which is invariably full of wood fragments. This suggests a storage function of the appendix as previously proposed by Morton (1970, 1978) and Saraswathy & Nair (1971). Morton (1970) considered debatable the function of the appendix as a site of primary breakdown of cellulose, and Morton (1978), reviewing the literature pertaining to the digestive processes in the Teredinidae, stated that there is no evidence to suggest that the appendix acts other than as a temporary store for unwanted material. Nevertheless, Bazylinski & Rosenberg (1983) revealed the presence of a microvillar border associated with the epithelial cells of the appendix of *Bankia setacea, Teredo bartschi,* and *T. navalis.* They suggested that this pocket has an absorptive function, rather than being a site of temporary storage of wood fragments as previously thought by Morton (1970, 1978) and Saraswathy & Nair (1971).

According to the criteria of Turner (1966), the mid-gut of *Nausitora fusticula,* which does not loop over the style-sac, is of moderate size. In this species the major typhlosole is lacking along the entire extension of the mid-gut, except at the bulbous region, and feces are not

eliminated as pellets. In addition to these characteristics, the presence of a moderate-sized appendix and of a slightly developed, uncoiled typhlosole of the appendix form some of the main characteristics considered by Turner (1966) as indicative of a predominantly suspension feeding habit. Wood is therefore probably of lesser importance in the diet of *N. fusticula.*

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The Veliger 41(4):366–368 (October 1, 1998)

THE VELIGER

A New Species of *Pristiloma* (Gastropoda: Zonitidae) from a California Cave

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Abstract. *Pristiloma* ***cavator,*** sp. nov., is described from Samwel Cave, Shasta County, California. *Pristiloma juniperum* Smith, 1957, is a synonym of *Pristiloma spelaeum* (Dall, 1895); *P. spelaeum* is regarded as a distinct species, not a subspecies of *Pristiloma subrupicola* (Dall in Packard, 1877). A prior lectotype designation for *P. spelaeum* is invalid.

INTRODUCTION

Shells of the following new taxon were collected by explorers of Samwel Cave, Shasta County, California, on several occasions between 1957 and 1959. Most are more or less eroded and/or encrusted with reddish-brown, calcareous cave deposit. Bird and mammal bones and other land snail remains from Samwel Cave have been thought to range from late Pleistocene to early Holocene in age (Miller, 1933; Treganza, 1964; Graham, 1967; Payen et al., 1978). Several other species of land snails recovered from deposits in Samwel Cave were later found living in the same area (Walton, 1970; Roth, 1981; Roth, unpublished data), and there is no obvious difference between the cave snail faunule and the Recent snail fauna. However, field work in the area by other snail biologists and myself has failed to locate living populations of this species to date. It is therefore described on the basis of cave shells. We might have suspected that the species was extinct, except that one specimen out of 121 examined contained dried-in remains of the animal.

The following abbreviations are used: ANSP, Academy of Natural Sciences of Philadelphia; BR, author's collection, San Francisco, California; CAS, California Academy of Sciences; FMNH, Field Museum of Natural History; SBMNH, Santa Barbara Museum of Natural History; USNM, National Museum of Natural History, Smithsonian Institution.

SYSTEMATICS

Family ZONITIDAE Mörch, 1864
Pristiloma Ancey, 1887

Type-species: *Zonites stearnsi* Bland, 1875; by subsequent designation (Baker, 1930).

Zonitidae with shell small to minute; discoidal, hemispheric with deep, convex base and spire scarcely raised, or depressed-helicoid; colorless, yellowish, reddish brown, or brownish olive, glossy, thin, transparent when fresh; with 3.5–7 closely coiled whorls. Umbilicus narrow to absent. Sculpture lacking in most species, except for weakly impressed collabral striae; some species with close, regularly spaced, radial grooves extending outward from suture, fading out at or above periphery. Aperture lunate; peristome simple or, less often, thickened within by weakly toothed transverse rib. Penial retractor muscle originating on floor of lung and inserting on epiphallus or summit of penis. Penis containing various forms of ridges or pilasters, but not spinelike papillae. Spermatheca and its duct usually well developed.

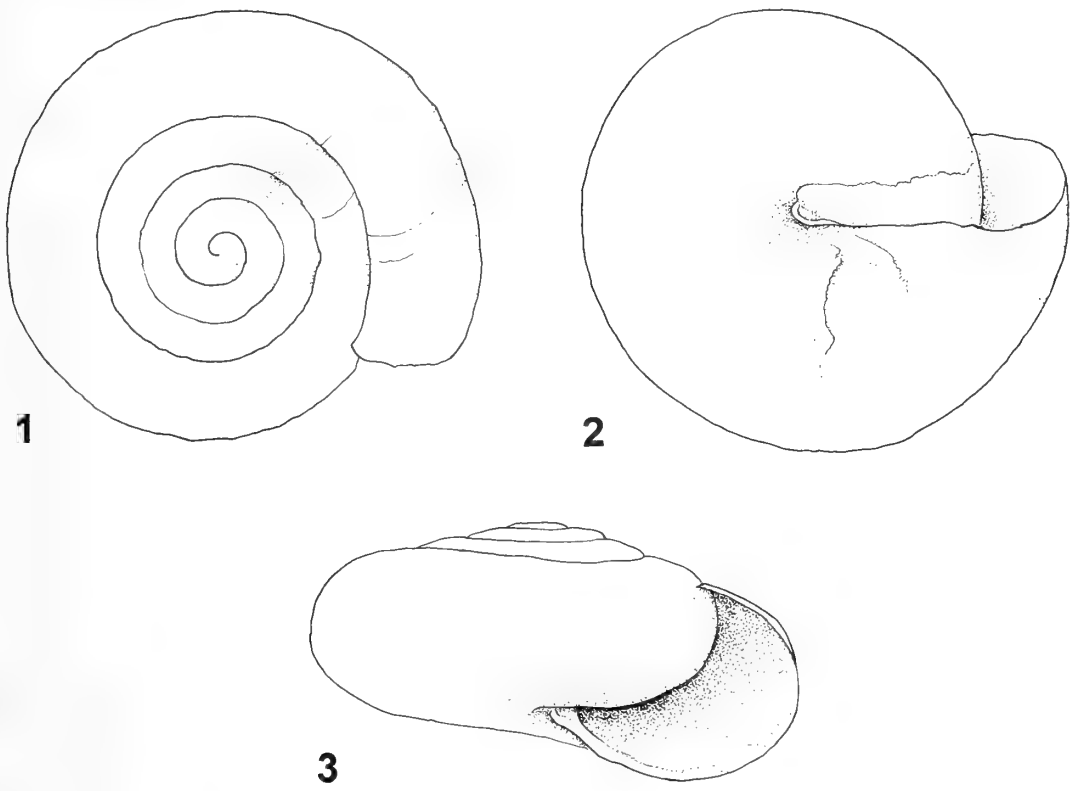
The genus ranges around the North Pacific rim from southern California to Japan, and inland in North America as far as Idaho, western Montana, and Utah. Seven other species are known from California; additional, unnamed species are under study.

Pristiloma ***cavator,*** sp. nov.

(Figures 1–3)

Diagnosis: A large, discoidal *Pristiloma* without umbilicus at any stage of growth; adult with inner end of basal lip joining with parietal callus to protrude as small callus tongue appressed over shell axis.

Description: Shell up to 5.0 mm in diameter, non-umbilicate, discoidal, with sloping shoulder; spire very slightly raised; with up to 4.7 steadily and regularly enlarging whorls; suture appressed but distinct; profile of spire whorls weakly convex. Periphery obtuse, looking as if slightly compressed toward shell axis. Base weakly convex, somewhat excavated centrally, crossed by shallowly sinuous, impressed collabral striae at irregular intervals, with extremely fine, close-set spiral striations apparent on well-preserved material; basal lip shallowly, doubly sinuous in basal view, produced in the middle. Aperture broadly lunate; peristome simple, not thickened; inner part of basal lip turned outward; extreme inner end



Explanation of Figures 1 to 3

Pristiloma ***cavator*** Roth, sp. nov. Holotype, SBMNH 144393. Top, basal, and apertural views. Diameter 4.9 mm.

joining with parietal callus to protrude as small tongue of callus appressed over shell axis. Parietal callus moderately thick, surface finely papillose. Shell solid for the genus, glossy and translucent when fresh, otherwise smooth and opaque white.

Dimensions of holotype: Diameter 4.9 mm, height 3.1 mm, whorls 4.6.

Type material: Holotype: SBMNH 144393, CALIFORNIA: Shasta County: Samwel Cave [SW¼ sec. 5, T. 35 N, R. 3 W, Mount Diablo Base and Meridian]. R. de-Saussure et al. coll. 5 June 1957.

Paratypes: CAS 112280 (2 specimens), BR 1915 (6), FMNH 293001 (2), SBMNH 144394 (12), USNM 860653 (2), ANSP 401179 (2), collection of Terrence J. Frest, Seattle, Washington (2). With same locality data as holotype.

Referred material: All, CALIFORNIA: Shasta County: Samwel Cave. BR 1909, R. E. Graham coll. 1958 (6). BR 1910, R. E. Graham coll. 1958 (1). BR 1911, R. E. Graham coll. 25 June 1959 (1). BR 1912, R. E. Graham coll. 10 June 1959 (1). BR 1913, R. E. Graham coll. 25 June 1959 (2). BR 1914, R. E. Graham coll. 25 June 1959 (2). BR 1916, "Area D," depth 0 ft 6 in [0.15 m], N. Slusser coll. 4–7 June 1957 (10). BR 1917, "Area D," depth 0 ft 6 in [0.15 m], N. Slusser coll. 7 June 1957 (42). BR 1918, R. E. Graham coll. 5–6 January 1957 (1). BR 1919, N. Slusser coll. 5 June 1957 (1). BR 1920, 90 ft pit, total darkness, R. E. Graham coll. 11 June 1958 (2). BR 1921, R. E. Graham coll. 25 June 1959 (1). BR 1922, R. E. Graham coll. 19 December 1959 (1).

Remarks: The subgeneric taxonomy of *Pristiloma* is based on characters of the reproductive system (Baker, 1931; Pilsbry, 1946; Riedel, 1980). Until living material of *Pristiloma* ***cavator*** can be collected and dissected, the species is assigned only to the genus in the broad sense. A phylogenetic analysis of the species of *Pristiloma* is now in progress.

As in most Zonitidae, there is no change in spiral growth trajectory or turning out of the lip in *P.* ***cavator*** at adulthood. It is therefore not obvious among the material at hand which shells represent adult individuals, and size characterizations run the risk of including ontogenetic variation. However, in the material at hand, the diameter of shells with 4.0 or more whorls ranges from 3.3 to 5.0 mm (mean of 31 specimens including holotype, 4.15 mm; standard deviation 0.414). Many of these have

the basal callus tongue well developed, which may indicate a definitive stage of shell growth.

Lot BR 1917 consists of 42 specimens in stages of growth from 2.0 whorls up and demonstrates that at no point in ontogeny does *P. **cavator*** have an umbilicus.

*Pristiloma **cavator*** differs from the smaller (ca. 2.5 mm diameter; Pilsbry, 1946) *Pristiloma johnsoni* (Dall, 1895) of the Pacific Northwest in that the last whorl is less than twice the width of the preceding whorl. It differs from other discoidal, white to translucent-shelled species, including the Californian *Pristiloma nicholsoni* Baker, 1930, *P. shepardae* (Hemphill in W. G. Binney, 1892), *P. orotis* (Berry, 1930), *P. spelaeum* (Dall, 1895), and *P. gabrielinum* (Berry, 1924), in having no umbilicus at any stage of growth. The tongue of callus formed by an extension of the inner end of the basal lip and the parietal callus is similar to that present in *Pristiloma subrupicola* (Dall in Packard, 1877) from Utah, Idaho, and Oregon (see Pilsbry, 1946: fig. 226), but *P. subrupicola* has a narrow umbilicus.

Pristiloma spelaeum has been regarded since its description as a subspecies or "variety" of *P. subrupicola.* I have examined 11 samples of *P. spelaeum* in the California Academy of Sciences and my own collection. None of the specimens shows development of a callus extension in the umbilical region. *Pristiloma subrupicola* is anatomically distinctive in having a vaginal caecum containing an elongate papilla, a muscular sheath covering the penis, and the vas deferens passing through the sheath so that the epiphallus forms a loop. The positions of the origin and insertion of the penial retractor muscle also are different from those of other known *Pristiloma* species (Baker, 1931), and some authors place the species in the separate genus *Ogaridiscus* Chamberlin & Jones, 1929 (Riedel, 1980). *Pristiloma spelaeum* has not yet been dissected. In the absence of information about its reproductive system and penial musculature, assigning it the status of a subspecies of the anatomically distinctive *P. subrupicola* assumes facts not in evidence; I therefore regard it as a separate species.

In his original description of *Pristiloma juniperum,* Smith (1957) compared his new species to *P. gabrielinum* but not to *P. spelaeum.* The characters by which he distinguished *P. juniperum* from *P. gabrielinum* are also found in *P. spelaeum,* and I regard *P. juniperum* as a synonym of *P. spelaeum.*

In the paper by Smith (1957), the original figures of *Pristiloma juniperum* are transposed with those of a purported lectotype of *Vitrea subrupicola* var. *spelaea* Dall, 1895 (i.e., *Pristiloma spelaeum*). Smith's plate 2, figures 4–6 actually depict the holotype of *P. juniperum*; plate 2, figures 1–3 depict *P. spelaeum.* In addition, Smith (1957) designated as lectotype of *Vitrea subrupicola* var. *spelaeum* a topotypic specimen (now CAS 055397) from the Henry Hemphill collection. There is no evidence that this specimen was ever seen by Dall, and therefore it cannot be part of the type lot. Smith's (1957) designation of it as a lectotype is therefore invalid, although the specimen might be a candidate for a neotype if Dall's original material is lost and the status of the species needs clarification. Boss, Rosewater, & Ruhoff (1968) did not report the location of any type material of *Vitrea subrupicola* var. *spelaea.*

Etymology: L., *cavator,* an excavator.

ACKNOWLEDGMENTS

I am grateful to the late Allyn G. Smith who placed this material, originally in his personal collection, in my hands for description. Terrence J. Frest commented on the manuscript and contributed information on the distribution of *Pristiloma* and *Ogaridiscus* in Oregon and Idaho.

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The Veliger 41(4):369 (October 1, 1998)

THE VELIGER

NOTES, INFORMATION & NEWS

Manuscript Reviewers for Volume 41 of *The Veliger*

The following reviewers contributed their time, effort, and expertise to evaluate manuscripts submitted during the course of assembly of Volume 41. The quality of *The Veliger* depends strongly on the voluntary assistance of independent reviewers such as these, and we are grateful to them.

D. W. Behrens, H. Bertsch, J. S. Bleakney, P. Bouchet, S. Bower, J. C. Britton, E. V. Coan, R. Collin, M. J. de-Maintenon, R. T. Dillon, Jr., K. C. Emberton, J. A. Estes, J. W. Forsythe, T. J. Frest, B. Fried, D. L. Geiger, F. Giusti, M. Haase, R. Hershler, C. S. Hickman, J. H. Himmelman, F. G. Hochberg, C. F. Ituarte, A. R. Kabat, D. R. Lindberg, G. L. Mackie, P. B. Marko, J. H. McLean, A. L. Metcalf, S. V. Millen, B. Morton, W. A. O'Connor, P. G. Oliver, D. K. Padilla, G. Paulay, T. A. Pearce, S. C. Pennings, R. S. Prezant, T. A. Rawlings, D. G. Reid, P. H. Scott, P. Sharkey, N. E. Strenth, J. D. Taylor, F. G. Thompson, N. Thompson, T. Ubukata, G. J. Vermeij, J. Voltzow, A. Warén, J. N. C. Whyte.

International Commission on Zoological Nomenclature

The following Applications were published on 30 June 1998 in Volume 55, Part 2 of the *Bulletin of Zoological Nomenclature*. Comment or advice on these applications is invited for publication in the *Bulletin* and should be sent to the Executive Secretary, I.C.Z.N, % The Natural History Museum, Cromwell Road, London SW7 5BD, U.K. (e-mail: iczn@nhm.ac.uk).

Case 2956—*Campeloma* Rafinesque, 1819 (Mollusca, Gastropoda): proposed conservation.

Case 3008—*Euchilus* Sandberger, 1870 and *Stalioa* Brusina, 1870 (Mollusca, Gastropoda): proposed designation of *Bithinia deschiensiana* Deshayes, 1862 and *Paludina desmarestii* Prévost, 1821 as the respective type species, with the conservation of *Bania* Brusina, 1896.

Case 3047—*Holospira* Martens, 1860 (Mollusca, Gastropoda): proposed designation of *Cylindrella goldfussi* Menke, 1847 as the type species.

The following Opinion concerning mollusks was published on 30 June 1998 in Volume 55, Part 2 of the *Bulletin of Zoological Nomenclature*. Copies of this Opinion can be obtained free of charge from the Executive Secretary at the address given above.

Opinion 1898. *Galba* Schrank, 1803 (Mollusca, Gastropoda): *Buccinum truncatulum* Müller, 1774 designated as the type species.

The Veliger 41(4):370–372 (October 1, 1998)

THE VELIGER

BOOKS, PERIODICALS & PAMPHLETS

Benjamin Delessert (1773–1847) et la Malacologie

by J. C. CAILLIEZ & Y. FINET. 1997. Bulletin de la Société Internationale de Conchyliologie (SIC) 19(3):1–44. ISBN 2-9402240-00-5.

This entire publication is dedicated to honoring Benjamin Delessert at the 150th anniversary of his death and to highlighting his contributions to malacology. He was born in Lyon, France, in 1773, a descendant of a famous Swiss family, just 16 years before the beginning of the French Revolution in 1789. He volunteered in the Paris National Guard in 1790, became a Captain and ultimately a colonel by the time of the first restoration of the monarchy. His allegiance to Napoleon during the Hundred Days ended his military career in 1815. He was, however, active in civilian life, when not called on military campaigns. A preface by M. Cuny summarizes his eclectic activities. To date, he is better known in France for being a banker in charge of the Banque de France for nearly 50 years and for creating the Caisse d'Epargnes, a savings system, which to this day all good kids in France are taught to use at an early age. He is also known for building the first beet sugar refinery, so important to Napoleon in surviving the British blockade. Napoleon awarded him the Legion of Honor and made him a baron. Additionally, he was a philanthropist who created hospitals and hospices, and he was a politician, representing the Seine department in which Paris is located.

From his youth, he was passionately interested in natural sciences, in botany and in malacology. He was a passionate collector of specimens as well as books. He accumulated a botanical library of over 6200 titles. Although he never described any genus or species, he was a great patron of other scientists. In gratitude, two botanical genera, *Lessertia* and *Delesseria* were named after him. As a malacologist, he began seriously to collect shells when he was 30. He collected fossils from the Paris basin and subsequently bought large collections, notably from Dufresne, Masséna, Hwass, and Teissier. He hired L. C. Kiener to curate his collection but subsequently replaced him with J. C. Chenu. As of 1825, the Hotel d'Uzès in Paris was at the same time his business offices for his banking activities, the residence for himself, his sister, and the family of his brother, François, and a large museum for his libraries and collections. By 1844, when he was 71 years old, the Benjamin Delessert collection was the most important collection in Europe, surpassing those of the Paris Museum and the British Museum. Concurrently, his malacological library contained practically everything that had been published for a century. As in botany, Benjamin Delessert never described any species or genera of mollusks. He never personally wrote any treatise on malacology. His contributions to malacology were as a patron, a collector, and a protector of famous collections. The bulletin lists 21 species of mollusks named after him. It also lists numerous publications by Hwass, Lamarck, Férussac, Deshayes, and others that referred to the Benjamin Delessert collection. At his death, his collections passed to his younger brother, François, and ultimately were donated to the Geneva Museum.

This bulletin is written in a somewhat flowery style, with numerous quotations, almost poetic, from other malacologists. I quote, in rough translation, one from Chenu: "Thus what is only a childhood game, an agreeable distraction, becomes a source of delicious souvenirs for the rest of one's life." One additional quote from M. Cuny, in his preface, would apply to so many of us malacologists: "Benjamin Delessert was part of this small fraction of persons who aid the world in making a few steps forward." Pleasant reading, interesting, with beautiful color prints of lovely shells.

Walter B. Miller

Towards a phylogeny of gastropod molluscs: an analysis using morphological characters

by W. F. PONDER AND D. R. LINDBERG. 1997. Zoological Journal of the Linnean Society 119:83–265.

Although a projected in-depth review of this important paper did not materialize, we cannot let this volume year pass without taking notice of it. This work is the first to put the whole of gastropod phylogeny on a rigorous, parsimony-driven footing, and an exemplary work of cladistics. All similar prior works have either addressed a subset of Gastropoda or a partial character set, or have lacked a full commitment to the cladistic method. The testable phylogenetic hypothesis generated on the basis of 117 characters and 40 taxa must be regarded as malacology's new standard for assessing relationships among gastropod clades and basically renders irrelevant former arrangements (e.g., those of Troschel, Bouvier, Thiele, Wenz, Yonge and others more recent) that have long influenced taxonomic and evolutionary thinking.

B. Roth

Non-marine Cerithioidea—Recent Work on Thiaridae and Melanopsidae

Evolutionsökologie und Systematik am Beispiel von Süß- und Brackwasserschnecken (Mollusca: Caenogastropoda: Cerithioidea): Ontogenese-Strategien, Paläontologische Befunde und Historische Zoogeographie [Evolutionary ecology and systematics, based on the example of fresh- and brackish-water snails (Mollusca: Caenogastropoda: Cerithioidea): ontogenetic strategies, paleontological data, and historical zoogeography]

by MATTHIAS GLAUBRECHT. 1996. Backhuys Publishers, Leiden. xvi + 524 pp. (incl. 25 pls.), 77 text-figs., 5 tables (hardbound). ISBN 90-73348-52-8. 180.00 Dutch Guilders (NLG; corresponding to approximately $117 U.S.).

As stated in the abstract (p. v), this monograph "aims, in an integrative approach, to synthesize phylogenetic systematics, evolutionary theory, ecology, palaeontology, biogeography, and malacology, using limnic gastropods as a case study. Following a general introduction and a short presentation of the focus of research (pp. 1–8), evolutionary ecology is shown to provide a framework that can help to elucidate new aspects, and function as a research program for acquiring more general perspectives in zoology [. . .]. *Evolutionary ecology,* as defined here, *aims to reconstruct the origin and alteration of the ecological interrelations of organisms and their respective environment in the course of evolution, as documented in the various biological features such as morphology, anatomy, physiology, ethology (thus affecting especially their phenotype, and biogeography).* The central part of this monograph is the study of 31 species in 23 genera of the freshwater and brackish-water Thiaridae and Melanopsidae, formerly united within the polyphyletic and nomenclatorially invalid 'Melaniidae'."

This work is the largely unmodified text of a 1994 Ph.D. dissertation completed at the University of Hamburg, Germany. Added were an English-language abstract and a German-language preface. The dissertation-style narrative meshes data, discussion, and philosophical interpretations. All this, combined with a rather complex writing style, make this work engaging reading material for a biologist with firm grounding in the German language ("German 101" will not begin to unravel this text). Matthias Glaubrecht has compiled an amazing amount of food for thought.

After introductory and materials and methods sections (pp. i–xvi, 1–29), the core of the monograph is arranged in seven main chapters, followed by an extensive literature section (pp. 447–476), an appendix, figure legends, and 25 black-and-white plates of shells, opercula, and radulae. The main chapters are:

C. Overview of the Cerithioidea (pp. 30–99): "A character analysis and evaluation—following Hennig's principle of weighting characters—establishes the foundation of this work" (p. v). Glaubrecht creates cladograms based on arguments of character evaluation that are thoughtfully outlined in the text. The result of this approach (something I would call "*narrative Hennigianism*") are hand-constructed trees with assumed character changes plotted on the branches, at times presenting alternative scenarios. Details of his cladistic methodology are not addressed (other than by the above reference to Hennig's "principle"). The author (p. 31) summarily dismisses computer-assisted analyses with a reference to a paper by Lorenzen & Sieg (1991, Z. zool. Syst. Evolut.-forsch., 29:466–472). No data matrix is presented that would allow a test for parsimony or consistency. Characters are numbered and explained in the text, but they are narratively used as apomorphies to support individual branches, without full disclosure of their states in the other taxa in the analysis. While this approach does not necessarily diminish the value of many arguments of character coding and hypothetical evolutionary relationships presented in this work, it certainly makes it difficult for readers who would like to change the taxon or character composition in a subsequent analysis. It makes it utterly impossible to test the robustness of the presented analysis.

Based on his own character evaluations, and using existing data of authors such as Richard Houbrick (anatomy; including previously unpublished manuscript data) and John Healy (sperm morphology), Glaubrecht arrives at a revised system for the Cerithioidea (p. 60), in which he groups the Procerithiidae, Cerithiidae, Diastomatidae, Planaxidae, and Thiaridae under the new name "Cerithiarida," and the Batillariidae, Potamididae, and Modulidae as its sister taxon "Multispirida." Cerithiarida and Multispirida, in turn, form a clade "Papillia." Papillia then stands in still-unresolved relationship to other members of the Cerithioidea, to which Campaniloidea is the sister taxon. It is concluded that fresh- and brackish-water biotopes have been repeatedly colonized by multiple evolutionary invasions within the Cerithioidea; at least three different lineages, the Melanopsidae, Pleuroceridae (+ Pachychilidae?), and Thiaridae, have crossed the brackish-water threshold and independently adapted to freshwater, "while the Potamididae form a monophyletic taxon that is hypothesized to have specialized itself in the estuarine biotope of tropical mangroves since the Cretaceous. Potamididae, which today live exclusively in brackish water, are not—as has been suggested before—the ancestors of all freshwater Cerithioidea; they represent a taxon that is not even near the stem line proceeding these limnic groups (p. vi)."

Other parts of this chapter, as part of Glaubrecht's approach to evolutionary ecology, deal with the life in nonmarine aquatic environments and discuss aspects of physiology, competition, niches, and radiation. This is followed by topics of reproductive biology (e.g., aphally, ovipary, ovovivipary, and vivipary), larval strategies, and poecilogony.

D. Morphology, anatomy, distribution, and ecology (pp. 100–296) describes and discusses the Thiaridae (= Melaniidae). The author has focused on African taxa (excluding those of the East African lakes, the focus of a separate study, see chapter F). The eight recognized Af-

rican genera (*Thiara, Melanoides, Pachymelania, Cleopatra, Pseudocleopatra, Potadomoides, Potadoma,* and *Melanatria*) are presented with much new anatomical information (with emphasis on their type species), and extensive discussions of reproductive biology and zoogeographical aspects are provided. Compared to these are the Asian thiarids (adding data on *Tarebia, Stenomelania, Fijidoma, Sermyla, Balanocochlis,* and *Neoradina*). A brief section dealing with American Thiaridae follows, addressing *Hemisinus, Pachychilus,* and *Doryssa.*

Agreeing with earlier work by the late Richard (Joe) Houbrick (to whom this volume is dedicated), Glaubrecht argues for a sister-group relationship of Planaxidae and Thiaridae (a clade for which he introduces the name "Incanabula"), and discusses the homology and associated reproductive strategies of brood pouches in this group. In the following section, the author argues against the *a priori* application of adaptive values (in the sense of economic or fitness principles) in determining the order of character state changes, and points to logical and practical problems in the study by Berthold (1991, Abh. naturwiss. Ver. Hamburg, [NF] 29:1–256; see Bieler, 1993, The Veliger, 36(3):291–297, for review). He proceeds to discuss monophyly and the presumed defining characters of Thiaridae and its three recognized subfamilies (Thiarinae, Paludominae, Melanatriinae). As part of his argument against the outdated concept of a "Melaniidae" group, Glaubrecht outlines characters (and differences) of the Melanopsidae, to which he counts *Melanopsis, Zemelanopsis, Faunus, Esperiania, Microcolpia,* as well as *Holandriana.* While he establishes his Melanopsidae as a clearly monophyletic group within the Cerithioidea, he argues that they are not closely related to the Thiaridae. The chapter closes with a case study of *Melanopsis* in the Mediterranean region, focusing on geographical distributions of shell and radular morphs, discusses ecophenotypy versus microgeographic speciation, and, finally, addresses *Melanopsis praemorsa* within the concept of a "superspecies." The latter step eliminates the problem of dealing with more than 200 species names (p. 296), an "elegant" solution that, however, still awaits corroboration through genetic population studies.

E. Comparative ontogeny (pp. 297–336) brings the ontogenetic data together and compares and discusses aspects of the ontogenies of the study groups with those of likewise fresh- and brackish-water neritimorphs, culminating in a critique of (K- and r-) life history theory.

F. Radiation of Thiaridae in the African Rift Lake system (pp. 337–349) discusses the previously "left out" East African lake taxa. Here the "dissertation character" of the work seems most troublesome. While providing a nice review of certain aspects of Lake Tanganyika thiarid biology, it apparently was conceived as a separate publication and regrettably does not deliver any degree of anatomical, morphological, or taxonomic treatment that would allow comparison to the "non-Rift" taxa of chapter C.

G. Paleontological data (pp. 350–404) covers much ground, from discussing the first "relevant" (p. 351) freshwater snail fossils from the Jurassic/Cretaceous border, to addressing the *Pyrgulifera* problem (the question of relationship between Recent Lake Tanganyika taxa and very similar upper Cretaceous forms). Again, the author provides a wealth of topics and data; he gives extensive examples of Cenozoic fossil records for *Melanoides, Brotia,* and *Melanopsis,* and then launches into discussions of species concepts.

H. Historical zoogeography (pp. 405–438): Here the author puts his results into a zoogeographic perspective, first concentrating on *Melanopsis,* and then on the family Thiaridae. Using paleogeographic data, he argues using vicariance and dispersal to outline various scenarios of *Melanopsis* evolution. The scenario presented for Thiaridae distribution (in South America, Africa, India, and Southeast Asia) remains superficial, considering that key taxa of the argument (such as the Neotropical *Cabaedomus* and *Hemisinus*) were not covered in the other parts of this monograph. Again, the argument would have been much more compelling if a more formal cladistic analysis, in this case involving area cladograms, had been attempted.

I. The evolution of fresh- and brackish-water Cerithioidea (pp. 439–446) "attempts to synthesize all the data compiled in this study into the most plausible evolutionary scenario, based on the cladograms and fossil data presented and highlighting the important steps, processes and mechanisms involved in the natural history of limnetic explorers among the Cerithioidea since their invasion of new adaptive zones in estuaries, rivers, and lakes. (p. xiii)." Here Glaubrecht focuses on the occupation of non-marine "adaptive zones," aspects of functional morphology (radulae and brood pouches), modes of reproduction, and the modifications from a free veliger larval stage. Citing the thiarids with their brood pouches as an example, he argues that a key innovation does not necessarily lead to great taxonomic diversification. As a goal for future work, the author points to a targeted search for the mechanisms that have led to radiations in the limnic environment.

The appendix provides further philosophical and nomenclatural discussion. The philosophical part (pp. 477–482), living up to the concept of a "classical" dissertation, provides a brief review of the epistemological induction versus deduction debate, explores the theoretical limits of scientific knowledge, and describes basic criteria for presenting heuristic hypotheses. The nomenclatural remarks (pp. 483–492) address various taxonomic problems in Thiaridae and Melanopsidae. This work does not introduce any new ICZN-regulated taxa, although several new higher-level taxa are proposed.

In summary, this massive work presents an important step toward our understanding of fresh- and brackish-water Cerithioidea. It would have been of even greater utility if the phylogenetic hypotheses had been presented in a more rigorous framework. Nevertheless, this monograph will be mandatory (albeit tough) reading for anybody interested in the group or looking for a recent discussion of "evolutionary ecology."

Rüdiger Bieler

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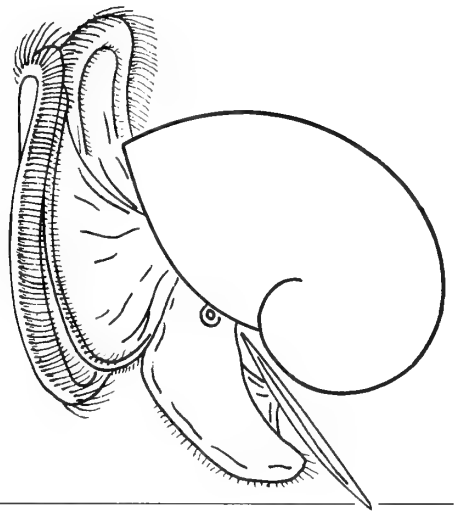

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